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THE RELATION OF GENETICS TO GEOGRAPHICAL DISTRIBUTION AND SPECIATION; SPECIATION. I.

INTRODUCTION¹

DR. LEON J. COLE
UNIVERSITY OF WISCONSIN

THE examination of almost any series of superficially similar objects or phenomena reveals that they differ in degree and that they may be arranged in simple or complex *graded* order. It is a common, and perhaps logical, assumption that those units which are closer together in the gradation, or which comprise divergent lines or groups, may be referred to similar or related causes. Especially if a temporal relation parallels the seriation, evolution is demonstrated as an objective phenomenon, aside from any commitment as to cause. Some of the most complete and striking illustrations of such evolution may be found in man's arts and artifacts—his language, apparel and arts, his implements of industry and war, and, by no means least, his ideas. Here it is evident that the progressive change is due to increased experience, based on preceding trials, to wider availability of materials due to new discoveries and inventions and to different needs as more complex situations arise ("emergent" evolution). The progression here

¹ Introduction to the combined symposia given at meetings of the American Association for the Advancement of Science, the first on "The Relation of Genetics to Geographical Distribution and Speciation" at Milwaukee, Wisconsin, before Section F—Zoological Sciences, on June 20, 1939, and the second on "Speciation" at Columbus, Ohio, before a joint session of the American Society of Zoologists and the Genetics Society of America, on December 28, 1939.

does not necessarily imply any change in the inherent human capacity but merely the ability of the individual or generation to profit by its own experience or by that of those which preceded it. In this it differs from organic series, where the superficial picture is strikingly similar, but in which each link in the chain is organically (materially, genetically) related to the one that precedes and the one that follows.

The early Greek philosophers were by no means blind to the objective evidence of evolutionary series, but their ideas as to causes were well at the bottom of the evolutionary scale of ideas on evolution. As Newman has aptly put it in speaking of Osborn's "From the Greeks to Darwin":

Professor Osborn studies the evolution of the evolution idea as a biologist would investigate the evolution of a species, using all of the available sources of evidence at his disposal. The fragments of ancient writing and the crude imaginings of early natural philosophers are the fossils of the evolution idea, many of them ancestors of modern principles; fragments of ancient or discarded ideas that still persist, though irrelevant to modern thought, are the vestigial structures that proclaim kinship between the past and the present; parallelisms between the development of ideas in the minds of independent thinkers do not prove plagiarism, but indicate common descent from the same ancestral ideas.

The earliest thoughts on evolution of which we have record are mostly vague speculations involving little more than the idea of change in the universe, as opposed to fixity. Apparently the "evolution question" was not a burning one in ancient Greece, as it came to be quite literally in Europe a few centuries later, but was a matter of academic concern primarily among a small group of philosophers and their disciples—the intelligentsia of the times. During the Dark Ages the theologians were in the saddle and if there were any original thoughts on evolution they remained discreetly unexpressed. With the revival of learning in the sixteenth century evolution again came to the fore and the battle about it, while shifting front from time to time, has since been continuous. As attention has become centered on the question of *how* evolution works we are prone to

forget that even to-day a great mass of people, indifferently or variously educated, are still convinced that it does not occur at all. Everything was made as it is or, at best, was created out of hand from time to time. True fundamentalism has no cross-fertility with evolution—it is a species strictly apart, and because of its survival into these times may be considered the lingula of the evolution-ideology family. It appears as the creation myth in the oldest strata of biological speculation and remains specifically unchanged through the centuries.

Evolutionary thought—the doctrine of progressive or at any rate of orderly or seriated change—early diverged into two “varieties” on the basis of “cause.” Empedocles apparently was satisfied to leave the process largely to chance, but later philosophers, and particularly Aristotle, impressed by the niceties of adaptation in animals and plants, felt there must be an underlying predetermined plan. Evolution proceeded, it is true, according to laws of nature, but these were but the workings of intelligent design. Thus the rival schools of materialism and of divine guidance, resulting in the age-long “struggle of science and religion,” got off to an early start. With biologists this has to-day become a question of mechanism *vs.* vitalism. Mechanism, though that is a poor name for it, holds that life and evolution might be explained according to the same laws and forces operating in the inorganic realm if we but knew enough about them; vitalism, on the other hand, would invoke the supervention of some wholly new and mysterious principle where life processes are concerned. While these two modes of thought are akin to attitudes on religion, in that the facts are not available definitely to prove one or the other, it is possible, fortunately, to proceed with investigation of the mechanics of evolution without awaiting a decision.

The species problem appears to-day, as it has for a century or so, to hold the master key to evolution. Darwin recognized this when he entitled his great work “The Origin of Species.” The necessity of change as

opposed to stability of organic forms was of course involved, and Lamarck had emphasized the importance of the environment in producing changes that were assumed to be directed and heritable. Darwin was not so much concerned with the way in which the variations arose—he rather took them for granted—as he was in how the favorable ones became selected, thus providing for the adaptation and consequent survival of their possessor. It was tacitly assumed by Darwin and by his successors that when there was considerable change it would result in new species, though geographic isolation was introduced as an important accessory. It is generally conceded that so long as the diverging forms remain in contact and are capable of interbreeding freely, specific difference can scarcely be attained. There is, therefore, not only the question of the *origin* of divergent forms but the equally important one of their *maintenance* as separate species.

Until early in the present century biologists were handicapped by lack of knowledge of the details of relationship of one generation to another which have been revealed by the rapid advance of genetic and cytological research. It has become apparent that variations, now generally called mutations, may arise in a variety of ways and that, in addition to gene change, chromosome number and arrangement (e.g., autopolyploidy) may be potent factors not only in originating new characters but in producing cytological “breeding barriers” which may be even more effective than geographical barriers in the attaining of species rank.

It will be noted that while this discussion has been around the species, no definition of it either as a concept or as a fact has been attempted. Probably no entirely satisfactory definition has been made or is possible until we have a clearer idea of what is involved. For practical purposes the taxonomist will of necessity use a different concept from one the geneticist might formulate on theoretical grounds or on the basis of breeding

or cytological tests not ordinarily available to the taxonomist.

Discussions of evolution had reached the point of being relatively sterile and largely academic until the newer knowledge of the cytological and genetic mechanics of heredity exercised its revivifying influence. The older methods of observation and speculation have since given way to definitely directed experimentation and logical exposition. Units of inheritance have been identified and located and by their manipulation and alteration a considerable measure of control over variation has been achieved. Varieties exhibiting greater differences than those ordinarily distinguishing related species in nature have been produced and maintained. Finally, by indirect manipulation of the chromosomes, new forms have been produced which meet that further strict requirement of true species, namely that, while themselves fully fertile, they are more or less infertile with their nearest relatives. The discovery of cases in which the same process has occurred under natural conditions means that the problem of the origin of species, at least in plants, has been partially solved. This is, however, apparently only one of several methods by which specific differences may arise and become genetically isolated. The intensive research on these problems that is now being prosecuted in many laboratories is abundantly attested by the following symposia on speciation.

SPECIATION OF FISHES¹

DR. CARL L. HUBBS
UNIVERSITY OF MICHIGAN

THE view-point of a naturalist will be expressed in this contribution. Even when laboratory experiments are recited, attention will constantly be focused on the origin and differentiation of forms in nature. The ecological aspect of speciation is considered no less vital than the genetic, since the environment is as indispensable in evolution as are the changing gene ratios. In this view a genetic type, whatever may have been its origin, has not speciated until through multiplication and inbreeding it has developed into one or more discrete populations, which have met and survived the strenuous ordeals of competition and adjustment in raw nature (Jordan, 1922). The production of a breed of chickens, or the isolation in the laboratory of a mutant strain of *Drosophila*, is not speciation—however significant the study of such processes may be in the analysis of the origin of species.

My treatment of the subject will reflect the thoughts not only of a naturalist but also of a specialist on one group, the fishes. Students of other groups, however, should find analogies which will render the remarks applicable to the animals which they study. Time does not permit the pointing out of these analogies, nor even a comprehensive treatment of speciation in fishes. Except for occasional examples, actual data can not be fitted in.

I

Recent studies in the systematics of fishes emphasize how intimately and how consistently the vital features of the environment are correlated with many if not most of the differences which characterize local races, subspecies, representative species and even genera.

¹ Read at a symposium on "The Relation of Genetics to Geographical Distribution and Speciation," before Section F—Zoological Sciences, American Association for the Advancement of Science, Milwaukee, Wisconsin, June 20, 1939.

The tie-up between specific environmental features and the characters of the evolving forms is particularly obvious in parallel variation, which therefore calls for attention. Critical studies of the variations of forms throughout their range are bringing to light an increasing number of character gradients or "clines," which are definitely associated with specific environmental gradients.

Attention has long been directed to the common tendency of fish forms of cooler waters to have a larger number of segments than those living in warmer waters. Thus, the number of parts increases toward the north, as also toward the open sea—for increased salinity has about the same speciation effect as decreased temperature. Forms of warmer water, and in the sea those of brackish water, typically have deeper bodies and larger heads than those of colder or more saline waters. I have indicated that increased numbers of somites, vertebrae, scale rows and fin rays and changes in body form tend to be correlated with retardations of development, whatever may be the cause for the slackening of the pertinent stage of development (Hubbs, 1926).

In some groups the reverse gradient in the number of certain meristic structures, as related to environmental temperatures, is the rule. In respect to the number of dorsal rays, for example, the Middle American viviparous cyprinodonts demonstrate a decrease not only toward the north but also toward the uplands or *tierras templadas*. Our recent systematic studies show that this latitudinal and altitudinal decrease in dorsal rays is a general phenomenon, and our breeding experiments prove that even small average differences in the number of rays are genetic.

Correlated gradients in characters of fishes and in the environment now appear to dominate the systematic ichthyological picture in the western fresh-waters of America. Whereas the ranges of the forms, as given, have been limited almost solely by the boundaries of

stream systems, our recent studies emphasize differentiations that are correlated with ecology rather than geography. Forms inhabiting smaller streams contrast with those living in large, swift rivers. The creek forms live in streams with a steep grade, but generally avoid fast water by frequenting the pools between riffles or by hiding in quiet pockets under and about boulders. The swift-river forms are more constantly facing the stress of current. In obvious adaptation, they tend to be larger and much more stream-lined fishes, with more terete bodies, sharper entering wedges and, particularly, with much slenderer caudal peduncles and longer and more falcate fins; and often with more rays in one or more fins or with smaller scales (which provide a smoother surface). Within *Formenkreisen*, series showing successive stages in these modifications are being demonstrated, and the same sort of gradients are repeated in different stream systems. Similar gradients, consistently in the same direction and with the same ecological correlations, have been identified in a considerable proportion of the more ubiquitous stream-inhabiting fishes of the West: in various species of *Catostomus* and *Pantosteus* among the suckers; of *Gila*, *Richardsonius*, *Lepidomeda* and *Apocope* (= *Rhinichthys*) among the minnows; of *Cottus*, the fresh-water sculpin; and probably of *Prosopium* and *Salmo* among the salmonoids. Parallel speciation correlated with current is obvious in other parts of the world, though less clearly pictured. The same character differences, depending more on consistency than on degree, in different cases define races, subspecies, species and genera.

Parallel speciation under the control of the environment has become strikingly evident during our recent studies of the fishes of the isolated waters of the arid American West. In the flowing streams, as already mentioned, the local forms of any species tend to have a stream-lined form, long and falcate fins and other characters enabling the fish the better to resist the current.

The riffle inhabitants are designed for bottom-life and bottom-feeding, having flat ventral surfaces and arched dorsal contours, and inferior, more or less horizontal mouths. In the isolated springs these special modifications of form are lost. The mouth tends to become larger and more oblique, fitted to engulf food organisms living at various water levels, rather than to grub around the stones of the riffles. In correlation with a general freedom from predation, the populations become dense and the sense organs reduced. Thus, the barbelled minnows lose their barbels, and the lateral line becomes obsolescent. The scales tend to drop their orderly arrangement and their deep imbrication, and to develop radii on all fields. In three originally unlike genera the terminal modifications along this speciational line have become so nearly molded into the same form, that they falsely appear to be very closely related.

Among the cyprinodont fishes, the desert-spring isolates tend to lose their pelvic fins. The loss has taken place in several regions and in several groups, and seems to be another example of the general tendency for animals to lose structures which are not of critical value under the environmental conditions to which they are subjected.

Parallelism is also evident in the evolution of lacustrine forms, fitted by their long and close-set gill-rakers and related changes in mouth structure to feed upon the rich plankton of lakes.

In studying the fresh-water fishes of the East Indies, I have been impressed with another character gradient which is repeated in different species, particularly of Cyprinidae. Races inhabiting the relatively sterile waters of mountain lakes and creeks tend to be elongate, terete, small-headed, small-eyed, and small-finned. Those of the lowland rivers, which abound in fertility, have deep though compressed bodies, large heads and eyes and expansive fins. These differences seem to be related to nutrition, and strikingly parallel the features which distinguish wild carp from the highly selected, fast-growing

Edelkarpfen of the German fish culturists. As usual in parallel speciation, the characters of the organism appear to have been brought into a harmonious adjustment with the usual or average features of its habitat. This relation seems to allow of normal development and life under the fluctuating environment with no undue strains or dangers. Successive adjustments of this sort provide a simple explanation for the origin of graded series of races (Hubbs, 1928).

Fishes of the very silty streams, as of the Great Plains, often if not generally, have smaller eyes but compensatingly better developed tactile organs than their congeners of clearer water. Particularly striking in the fishes of such darkened waters are the sense organs which appear to serve as current detectors. (This problem is being studied by my student, George A. Moore.)

The increased development of lateral-line sense organs and the increased flabbiness of deep-water fishes constitute a well-known and long-appreciated character gradient. The uniformity with which this gradient has been developed along many lines of evolution, and the strictness by which it is correlated with the environment, are truly remarkable.

Parallel modifications for life in lesser depths are perhaps of more significance in the study of speciation, since the connecting links are less liable to be broken. In many *Formenkreisen* there are littoral forms (races or species) which are boldly colored with generally brown tones, have thick skeletons and spines and small eyes. Their representatives in the twilight zone of moderate depths are paler and redder (therefore inconspicuous where red light rays are lacking), have thinner bones and spines, larger eyes and often better developed sense organs. Offshore pelagic derivatives are characterized in general by their metallic blue colors, terete bodies and small fins.

The more or less complete degeneration of the eyes in truly hypogean fishes is emphasized as a virtually uni-

versal phenomenon by my recent discoveries of five new blind fishes in the caves and artesian waters of North America, and by a summary treatment of the known cave and blind fishes (Hubbs, 1938). Something that is inherent in life in absolute darkness not only permits but forces the degeneration of the eyes and of pigment. The hypothesis is often proposed that the loss of these structures in cave fishes is an adaptation in that it conserves energy in a habitat where food is scarce, but this idea fails to explain why the nutrition-bathed entoparasites have likewise lost their eyes and pigment. I have suggested that such degenerative speciation may be the result of repeated mutations, in the total absence of selection, and have computed some possible rates of speciation on this basis.

Parallel speciation among fishes is nowhere more strikingly shown than among the lampreys (Hubbs, 1925; Hubbs and Trautman, 1937: 9-14). Again and again the parasitic lampreys have evolved into non-parasitic forms, through the elimination of the adult-feeding stage, the reduction in adult size and the degeneration of the intestine, teeth and mouth. Extreme end stages are confusingly alike, though clearly of diverse origin. The evolution of the non-parasitic or brook lampreys has been correlated with life in small streams, where a suitable food supply in the way of large fish is scarce or seasonal.

The tendency for such correlated gradients in characters and in the environment to be repeated again and again in the same direction, must be basic to an understanding of speciation. Any theories of species formation that fail to consider and explain the intimate tie-up between habitat and characters must remain at least incomplete. Whether the correlation results from some form of environmental determinism, or from the selection of an appropriate habitat by forms newly speciated through unadulterated genetics, does not appear to be a very real, general problem to those of us who look on

speciation as a definite interplay between the organism and its particular environment. In some types of habitats, for example, in caves, speciation no doubt continues under environmental conditions so uniform as to preclude any preadaptation followed by the selection of habitats, except perhaps in the first stages of the orthogenetic process. In other places, as in a newly invaded territory, an organism no doubt tends to settle in environments to which it is adjusted, in the sense that it shows there a high rate of survival. In general, however, the adaptation of an organism to its environment must be perfected through adjustments in characters, interwoven with the selection of suitable niches. And it may well be emphasized that the selection of a habitat to which a given form is fitted is in itself a form of natural selection, usually with some physiological speciation, and always involving the perpetuation of that which is in harmony and the elimination of that which is out of adjustment.

In the pragmatic sense, natural selection in my opinion is clearly an essential basis of speciation as well as of general phylogeny. Opponents of this view do not take into due consideration the relatively recent evidence that extremely slight selectional advantages lead in time to speciation. They neglect the overwhelming evidence for compensative adaptation when they claim that a form with a given character has no selectional advantage because other populations lacking this alleged advantage succeed equally well, even in the same habitat; the species or group less well-endowed in regard to this character will almost surely be found more propitiously endowed in some other respect. In arguing that no advantage should be attributed to very slight, perhaps only average differences in such characters as those of meristic numbers of fin rays or scales, those combating natural selection give too little weight to the evidence that such differences are the direct consequences of vitally important changes in the rate of metabolism and the rate of development (Hubbs, 1926). They side-step

the indication that multiple effects of genes or linkage bind certain characters with some unexpected features that do have survival significance. Naively, some have held that the so-called non-adaptive, specific characters may have come into expression because they are genetically associated with an increase in fecundity. How much more objective it would be to lay stress on the selectional advantage of the increased rate of reproduction as the essential change, even though it be hidden from view, and to regard the associated morphological change as a secondary consequence, which in itself might have been of neutral or even negative significance. The essential test of selection is the survival and increase of gene or genes which in any way favorably affect the chance that the individuals so endowed will survive to reproduce in the environment in which they find themselves. In considering the "survival of the fittest," more emphasis perhaps needs to be placed on "survival," less on "the fittest."

Since virtually identical speciational changes related to the environment occur so repeatedly along unrelated phyletic lines, we can not overlook the probability that a single form may independently become modified more than once into derivatives that are indistinguishable one from another. Therefore, we have as a rule no way to prove that a subspecies or species with environmentally correlated characters is not of polyphyletic origin.

II

Through a study of hundreds of specimens of natural fish hybrids representing dozens of interspecific and often intergeneric combinations in several families, I have become convinced that as a very general rule the systematic characters of fishes show blending inheritance. The same sort of inheritance seems to operate when subspecies and races of fishes have crossed. A large body of information indicates that simple Mendelian segregation very seldom results when crosses have been made between natural forms of any vertebrate group.

Geneticists may object to this view as having been based on a study of presumed hybrids collected in nature. In mating experiments, however, the same results have been obtained for a number of interspecific crosses, in several families. This has been well demonstrated, for example, in our work on hybridization in the sunfishes (Centrarchidae), in which the experimental results stand in fine accord with the observational (Hubbs and Hubbs, 1932, 1933). Data on the viviparous killifishes (Poeciliidae) are much more extensive though as yet largely unpublished. Since we have made dozens of crosses among these fishes, particularly in the genus *Mollienisia*, we feel safe in announcing the following results:

(1) The genetic behavior is similar whether the crosses are between races, subspecies, species or genera.

(2) In almost all characters the F_1 hybrids from either reciprocal cross are precisely intermediate between the parent forms, so that they may be represented by the Galtonian fraction, $\frac{1}{2}$.

(3) Backcrosses in either direction yield offspring just intermediate between the hybrids and the given parent form, so that we may designate them as $\frac{3}{4}$ hybrids on the generally discarded Galtonian system.

(4) Successive backcrossings in the same direction yield $\frac{7}{8}$ hybrids, $\frac{15}{16}$ hybrids, etc.

(5) By this method the one parent type is reconstructed, in a form indistinguishable from the original (except at times for certain color features having little or no systematic significance).

(6) In the successive backcrosses toward one parent form there are never produced definite throwbacks toward the other parent form, nor is any marked increase in variability apparent. Since thousands of fish have been obtained in such matings, we would need to argue that a very high number of multiple factors is operating—if multiple factors are involved.

(7) Similar results and conclusions come from multiple mating experiments, in which as high as five species and twelve subspecies or races have been combined in

single individuals. The consistency of characters within such broods is amazing; the variability seems to be no greater than in the stocks of any of the constituent forms. The characters behave in such strict conformance with the Galtonian scheme of inheritance that one can, for instance, compute rather precisely the number of dorsal rays in the final multiple hybrid by striking theoretical averages through the complex mating chart, starting only with the known average value of each form as it is introduced into the multiple matings. Such characters as position of fins, form of body and coloration appear to show a similar type of inheritance.

(8) F_2 hybrids, on the average, follow the same fractional system of inheritance, and remain consistently intermediate between the parent forms, when the whole organism is considered, though showing a considerable increase in variability when any one character is analyzed. In apparent contrast with the results of successive backcrosses and of multiple matings, a limited number of multiple factors seems on this basis to be involved.

(9) For those interested in the type of sex determination and in fertility relations, it may be stated for *Mollienisia* and related genera that the male hybrids are the more fertile in interspecific and intergeneric crosses, and that graded degrees of fecundity exist. In general the fertility of the hybrids in each sex is directly proportionate to the closeness of relationship between the parent forms, with irregularities that seem to be due to the differential adaptability of the forms to aquarium conditions. Incidentally, we find in these observations no evidence to support the hypothesis advocated by Shull, that sudden breaks in fertility relations are essential in speciation.

In stressing the general absence of simple Mendelian segregation in the systematic characters of vertebrates, I do not overlook the evidence that many examples of unit factors have been demonstrated in this group. In the poeciliid fishes, for example, the work of Gordon and Fraser (1931) has shown that many color markings exist-

ing in nature show simple genetic behavior. In general, however, the characters with such genetic basis occur hit and miss through populations without sufficient consistency to be of much systematic significance. Varied ratios of the phases may characterize populations and forms, but the presence or absence of a given phase character in itself is usually not a systematic criterion. The distinction probably does not always hold between the systematic characters showing blending inheritance on the one hand and the phase characters with a simple genetic basis on the other, but the evidence is piling up to indicate that the distinction is a real and valuable one. Let me illustrate the difference by reciting the origin of the red swordtail of aquarists. No red phase of the swordtail genus *Xiphophorus* has been taken in nature and none seems to have originated by mutation in captivity, but the red phase does occur in the related genus *Platypoecilus*, which hybridizes rather freely with *Xiphophorus*. The hybrids produced by mating a *Xiphophorus* with a red *Platypoecilus* are, in part, of an undiluted red, though intermediate in the ordinary systematic characters, such as form, number of rays, and structure of gonopodium. Red hybrids mating back to *Xiphophorus* produce three-quarter hybrids of which, however, a certain proportion is red. One or two more backcrossings then reconstruct the swordtail, in all respects other than the red clothing.

Nor do I overlook the evidence that many systematic characters in plants and insects have been proved to have a simple Mendelian basis. Perhaps the high number of non-duplicated chromosomes characteristic of vertebrates is in part responsible for the blending inheritance generally shown by the systematic characters.

In dealing with speciation among the vertebrates, much of uncertainty and incompleteness must be attached to any theories or discussions which do not take into consideration the evidence that blending generally features the inheritance of racial, subspecific, specific and generic characters. The biological significance of this circum-

stance has been illuminatingly treated by Sumner (1932), and is now receiving the consideration of Dice, in connection with their intensive studies of speciation in the mice of the genus *Peromyscus*.

III

The close correlation between environment and characters is particularly well shown where speciation is released from the deadening effect of biotic saturation. In the great rift lakes of Africa, and in some other geologically recent lakes over the world, radiative adaptation has almost explosively filled the newly created niches (Worthington, 1937; Herre, 1933, etc.).

Evidence is accumulating, particularly from our analysis of the fish faunas of the isolated waters of the West, to indicate that speciation with environmental correlations may be unexpectedly rapid, when the swamping effects of outbreeding are eliminated. In several isolated waters, evolution has proceeded far enough to produce new subspecies within what appears to be a few hundred years, at most, a few thousand.

IV

Years ago the Scandinavian ichthyologist, Smitt, emphasized the tendency toward parallelism in the observed differences between species, between sexes and between growth stages, but the time was apparently not ripe for a general appreciation of this significant phenomenon. In our own recent work these parallelisms are becoming very apparent. In 1927 I pointed out that the environmentally correlated differences between forms typically involve varied degrees of completeness of the processes of growth and differentiation. Thus systematic differences are definitely linked with age variations. It will hardly need to be stated that sexual dimorphism to a large degree can be brought into the same picture.

As an example of the multiple correlations in differentiation, I will cite the situation in the Ameiuridae, or North American fresh-water catfishes. Aside from a general tendency for a northward decrease in the number

of anal rays, most of the racial differences within the species involve an increase toward the north in the thickness and depth of the body, along with a decrease in the length and roughness of the fin spines. These variational gradients are repeated in the same direction in different species of *Ameiurus* and in species of other genera in the family. The same differences distinguish females from males, and young from adults. Species as well as races are involved, since, for example, *Ameiurus nebulosus* differs from *Ameiurus melas* in the same way that the southern race of either species differs from the northern one, or the female from the male, or the young from the old. We thus find a striking and general parallelism in the variational gradients, which may be thus expressed:

A. nebulosus → *A. melas*
Southern race → northern race
Female sex → male sex
Young stage → old stage.

In respect to coloration we find a reversed gradient, in that *Ameiurus melas* is the more juvenile, as are the northern races and the males, so that the gradient formula for this character becomes:

A. nebulosus → *A. melas*
Southern race → northern race
Female sex → male sex, all as before; but
Old stage → young stage.

From these empirical facts, if not from pure biological reasoning, we are led to expect that similar if not identical biochemical processes will be found to be involved in all spheres of differentiation—ontogeny, sexual dimorphism and direct environmental effects, as well as speciation. This expectation, perhaps, has often been appreciated, but I think not commonly considered so concretely and not utilized in developing a field of research—the comparative physiology and biochemistry of differentiation. The stage is now set for this basic development.

The very general and striking tendency toward parallel genetic variation, with environmental correlations, at least suggests that relatively few and perhaps relatively simple biochemical processes are usually involved in

speciation. That modifications directly induced by the environment rest on much the same biochemical basis as the genetically controlled adaptations is suggested by a number of observations. The direct modifications usually affect the very characters which show genetic adaptation, and often in the same way. For example, factors which accelerate (or retard) a given developmental stage directly induce structural modifications in the same direction as those which are correlated with inherited differences in the rate of development (Hubbs, 1926 and 1934, and papers there cited).

CONCLUSION

As a result of our recent studies on fishes, including breeding experiments as well as systematic and variational studies of natural forms throughout their range, weight is constantly being added to the theory that speciation is no aimless wandering of genes through the organic world, but rather an orderly adjustment under the rigid control of the environment.

LITERATURE CITED

- Gordon, Myron and Allen C. Fraser
1931. *Jour. Heredity*, 22: 168-185, 8 figs.
- Herre, Albert W. C. T.
1933. *AM. NAT.*, 67: 154-162.
- Hubbs, Carl L.
1925. *Pap. Mich. Acad. Sci., Arts and Letters*, 4, 1924: 587-603, figs. 16-22.
1926. *AM. NAT.*, 60: 57-81.
1928. *Anat. Rec.*, 41 (Suppl. 1): 49.
1934. *AM. NAT.*, 68: 115-128.
1938. *Carnegie Inst. Wash. Publ.*, 491: 261-295, pls. 1-4.
- Hubbs, Carl L. and Laura C. Hubbs
1932. *Pap. Mich. Acad. Sci., Arts and Letters*, 15, 1931: 427-437.
1933. *Ibid.*, 17, 1932: 613-641, figs. 69-71, pls. 64-65.
- Hubbs, Carl L. and Milton B. Trautman
1937. *Misc. Publ. Mus. Zool. Univ. Mich.*, 35: 1-109, figs. 1-5, 1 map, pls. 1-2.
- Jordan, David Starr
1922. *Science* (n.s.), 56: 448.
- Sumner, Francis B.
1932. *Bibliogr. Gen.*, 9: 1-106, figs. 1-24.
- Worthington, E. B.
1937. *Intern. Rev. Ges. Hydrobiol. und Hydrogr.*, 35: 304-317, 1 map.

ECOLOGIC AND GENETIC VARIABILITY WITHIN SPECIES OF PEROMYSCUS¹

DR. LEE R. DICE
UNIVERSITY OF MICHIGAN

THAT individual characters seldom are uniform throughout the whole range of any species or subspecies is well appreciated by every taxonomist. Every species and every subspecies (the geographic race of the vertebrate zoologist) varies in its characters from place to place, and more or less distinct local races or families may occur in restricted areas. A local race which is fairly uniform and distinct in its characters and which occupies a definite geographical area will probably be described as a subspecies, even if the size of the population is small. Most local races, however, are variable in their characters and are not sufficiently distinct to be recognized in taxonomy.

The variability of subspecies and species, at least in mammals, is not primarily due to a direct influence of the environment upon the individual animals, but is based upon variations in heredity. This was first demonstrated by F. B. Sumner (1932: 28-30) in his classic studies of *Peromyscus*. My own studies of the genus confirm and support Sumner's conclusions.

The considerable amount of local variability within a single subspecies is well shown by the eastern woodmouse, *Peromyscus leucopus noveboracensis*. The body dimensions and pelage color of these mice vary greatly from place to place in the eastern United States, though all are assigned to this one form (Dice, 1937: 17-31; and 1939: 3-16). Populations of these mice living in three different woodlots in the near vicinity of Ann Arbor, Michigan, differ about as much from one another in body dimensions and in pelage color as do populations of the subspecies living hundreds of miles apart.

¹ Read at a symposium on "The Relation of Genetics to Geographical Distribution and Speciation," before Section F—Zoological Sciences, American Association for the Advancement of Science, Milwaukee, Wisconsin, June 20, 1939.

The characters which distinguish some local races may have arisen through inbreeding in partially isolated habitats, with consequent chance elimination of certain genes and fixations of the remaining gene combinations (Wright, 1932: 360-362). New mutations arising in isolated or partially isolated small populations may also affect the character of the local stock, especially if the same mutation recurs frequently. Little is known, however, about the rate of elimination of genes or the rate of mutation of new characters of the sort which distinguish races, and, consequently, the effectiveness of these processes for evolution within species can not now be evaluated.

Not all the variability within species can be the result of chance alone, for it has been demonstrated that there is a tendency for the pelage color of ground-dwelling small mammals to be correlated with the soil color of their habitat (Dice and Blossom, 1937: 106-108). The pelage colors of *Peromyscus* are, at least in major features, inherited and accordingly it must be concluded that the environment in some way controls in part the heredity of these mice.

The correlation between the pelage color of small mammals and the soil color of their habitat is particularly well shown in the western arid regions, where there is considerable diversity of soil colors and usually only a scant cover of vegetation. On isolated buttes or beds of black lava the rock-inhabiting species of small mammals tend to develop dark-colored local races, while on pale-colored granite mountains or on pale-colored sands the mammals tend to be pale in color. For instance, on the Tularosa Malpais, a lava bed in the Tularosa Basin of southern New Mexico, five species of saxicolous mammals have developed black or blackish local races. These include the rock-squirrel, rock pocket-mouse, juniper-mouse (*Peromyscus nasutus*), and two species of woodrat. In addition, some individuals of the cactus-mouse (*Peromyscus eremicus*) are here dark in color, perhaps indicating that a dark-colored race of this species is now in process of formation.

The same trend for a correlation between pelage color and soil color occurs also in humid regions. The mice living on isolated sand beaches both along the Pacific (Sumner, 1917: 173-185) and Atlantic coasts (Dice, 1939: 12-15) tend to be paler in pelage color than their brethren living on dark-colored inland soils. This trend is particularly striking in the beach-mice (*Peromyscus polionotus*) of Florida and adjacent states. The mice of this species which live inland on dark-colored clays are dark buff in color, while the mice living on the pale-colored sand of the beaches are pale in color. On Santa Rosa Island, just off the coast of Florida in the Gulf of Mexico, the mice are extremely pale, almost white in color (Sumner, 1926: 149-184).

The dark colors of animals living in heavy forests and the pale colors of desert animals were noted long ago by naturalists, and numerous hypotheses have been proposed to explain this correlation. It is now clear that the dark colors of forest animals are only indirectly correlated with the heavy rainfall, with the high humidity of the atmosphere and with the density of the vegetation. In regions of heavy rainfall it will of course usually result that there is high atmospheric humidity and a rich cover of vegetation. Part of the vegetation falls to the ground each year and produces humus in the soil. The addition of the humus gives the soil a dark color, which the ground-inhabiting animals tend to match. The result is that in humid regions many of the animals are dark in color. Contrariwise, in the desert the vegetation is scanty and little humus accumulates in the soil, which, accordingly, is pale in color. Here, in correlation with the color of the soil, the animals tend to be pale in color.

The parallel production on entirely separated lava beds of somewhat similar dark-colored races of *Peromyscus* and of other small mammals, and likewise the production of pale-colored races on isolated areas of pale-colored soils can only mean that pelage color has some important relation to the life of the animals concerned. It is proba-

ble that the pelage colors of many races have been produced by natural selection, although this has not been proved in any particular instance. To our eyes, at least, most small mammals, when viewed from above in their natural habitat, appear concealingly colored.

The body size and proportions of *Peromyscus* are probably also of importance in the life of the animals, but we know little about the adaptive value of these features. We do not know, for instance, whether or not a tail which averages ten millimeters longer in one race than in another really makes much difference to the individual mouse. Certainly there is no such obvious correlation between body proportions and type of habitat as is true of color. Nevertheless, forest-dwelling *Peromyscus* have, in general, longer tails, and larger feet, perhaps correlated with their semi-arboreal habits, than do the prairie mice. Furthermore, there seems to be a tendency for desert mammals to have proportionately larger ears than forest or prairie forms. In the pocket-gophers of the Great Basin a correlation of body size with soil type and with the altitude of the habitat has been noted by Davis (1938: 338-342). It seems certain therefore, that, though still little understood, there are at least some general correlations between the body size and proportions of mammals and the character of the environment.

The above evidence indicates that the pelage color and body dimensions of small mammals are at least in part correlated with certain features of the environment. Color and size are the characters on which most geographic races of mammals are distinguished, and we are forced to conclude that, contrary to the statements in some text-books, a considerable number of taxonomic characters are influenced by the environment and are presumably adaptive.

A common ancestry for all the members of a subspecies is generally assumed by taxonomists. If a particular subspecies has now a discontinuous range, it is assumed that at some former time the range was continuous.

Thus, of the dark-colored subspecies *Peromyscus maniculatus rufinus*, which occurs in the forests of the Colorado mountains and also on isolated mountain-tops in Arizona and New Mexico, it has been assumed (Merriam, 1890: 20-21) that the range of the form was continuous during the glacial period when heavy mountain forests are presumed to have come low enough to connect together all the now isolated sections of the subspecies.

Let us now examine a particular local race within the subspecies *rufinus* to determine the conditions under which it exists. On the upper north slope of Mt. Lemmon, the highest peak of the Santa Catalina Mountains of southern Arizona, there occurs a small area of heavy Douglas fir forest. In this forest the deer-mouse is abundant, and on the humus-filled, dark-colored soil it is very dark in pelage color. It is accordingly assigned to the subspecies *rufinus* (Dice and Blossom, 1937: 48-50, 88-89). The total area on Mt. Lemmon covered by dense Douglas fir forest and inhabited by these dark-colored mice does not exceed one square mile in area. Surrounding the area of Douglas fir on Mt. Lemmon there is a belt of yellow pine forest, much more arid in type, and inhabited by a few deer-mice, which, at least at Summerhaven, are paler in color than those from the Douglas fir association, but which must nevertheless be referred to the subspecies *rufinus* (Dice, 1938: 17-18). At a still lower level on these mountains there is an encinal belt of oaks and junipers where I failed to secure any mice of this species though they probably occur rarely. Still lower, on the north side of these mountains only, there is a belt of arid grassland in which deer-mice are rare. Here the mice are a pale buff in color, and are accordingly assigned to the subspecies *sonoriensis*, which is characteristic of the pale soils of arid areas. Still lower, surrounding the bases of the mountains, is the desert belt, in which no mice of this species have been taken.

The dark-colored local race of *rufinus* living in the Douglas fir association on Mt. Lemmon constantly inter-

breeds, we may be sure, around the margins of its habitat with the paler colored local race inhabiting the yellow-pine association, and which in its turn undoubtedly interbreeds with the very differently colored subspecies *sonoriensis* occupying the nearby arid grassland belt. Under these conditions the mice living in the Douglas fir forest must constantly interchange hereditary factors with the surrounding populations. A deer-mouse can travel a distance of slightly over two miles in about two days (Murie and Murie, 1931: 203) and a deer-mouse could, therefore, if it wished, cross the whole major area of Douglas fir association on Mt. Lemmon in a single night. In the face of constant interbreeding with and immigration from the surrounding populations the local dark-colored race on Mt. Lemmon could not possibly long remain distinct except as the result of some process favoring the dark color. There is a suggestion, furthermore, that selection for dark color is in this situation rather rigorous.

If, as is strongly indicated, selection is essential to the continued existence of the dark-colored local race in the Douglas fir forest on Mt. Lemmon, does not this agency sufficiently account for the production of the race? I believe that selection, possibly aided by local mutation, actually is sufficient to produce this local race and that the hypothesis of a former extensive Douglas fir forest continuous with the forests of the Rocky Mountains is unsatisfactory. The dark-colored local race on Mt. Lemmon can not possibly be explained solely as a glacial relict.

In the Douglas fir forest on Mt. Lemmon the deer-mice were, when I studied the habitat, much more abundant than in the surrounding associations. This would result in considerable inbreeding within this local population. On the other hand, the population there is sufficiently large so that no tendency for immediate fixation of characters would be anticipated. In this flourishing population new characters would be expected to arise from time

to time by mutation, and other characters would constantly be introduced by interbreeding with the surrounding populations. Under these conditions, if we assume, as we must, that selection of some sort is operating to favor the darker colored individuals, we would seem theoretically to have satisfactory conditions for rapid evolution.

Dark-colored local races of mammals, similar to the one on Mt. Lemmon, occur on other high mountains in the Southwest, such as on the Chiricahua Mountains (Dice, 1938: 7-18), and it may be assumed that these local races have in general originated at the places where they now occur. If this be true, the subspecies *rufinus* as now recognized has had a polyphyletic origin, and the similarities of the several isolated populations making up the subspecies are due to parallel development, presumably in response to similar types of environment.

Additional evidence for parallel evolution within a subspecies of deer-mouse is presented by *Peromyscus maniculatus artemisiae* in southeastern Washington and adjacent states. This subspecies occupies the mountains and the higher parts of the Columbia Plateau north of Snake River in Washington and Idaho, and reappears on the Blue Mountains south of the river in Washington and Oregon. Snake River, however, is a barrier to the distribution of these mice which must have been in existence before the Blue Mountains were elevated. In the canyon of Snake River, at least at Lyons Ferry, the subspecies north of the river is *artemisiae*, while south of the river a different subspecies, *gambelii*, occurs. It seems certain, therefore, that the *artemisiae* of the Blue Mountains have had an origin largely or entirely independent of those assigned to the same subspecies from north of Snake River (Dice, 1939: 16-19).

Some subspecies occupy a narrow but very extended range. Such is *Peromyscus maniculatus gambelii*, which extends from interior Washington to Baja California (Osgood, 1909, pl. 1). This is an extreme range of over

1,200 miles. Along its western border, from San Francisco Bay northward, *gambelii* interbreeds with the dark-colored races *rubidus* and *oreas* and perhaps *artemisiae*. On its eastern border, north to Snake River, it interbreeds with the pale-colored race, *sonoriensis*. It is impossible to believe that *gambelii* in its long narrow range and with constant interbreeding on both sides with races of different color from itself, could long maintain its characteristics by the impetus alone of its original hereditary constitution, even if it should ever have had a uniform heredity throughout its whole range. It seems to me most logical to assume that its range and characters are determined largely by the fact that it lives in a strip of territory intermediate in type of environment between the heavy forests inhabited by the dark-colored races on the west and the arid areas inhabited by the pale-colored *sonoriensis* on the east, and that accordingly we have here a race, *gambelii*, of intermediate color and intermediate body proportions. In other words I conclude that the environment determines the characters of *gambelii* as it does those of the other races of *Peromyscus* which have been critically studied.

Mice which appear alike in pelage color and in body proportions may not necessarily have the same hereditary constitution. Tones of pelage color which are indistinguishable to our eyes may be produced by different combinations of genetic factors. For instance, the several types of dilution in the house-mouse and in other laboratory rodents may produce animals which appear alike or nearly so. Body dimensions are known to be in some laboratory animals controlled by multiple factors, different combinations of which theoretically can produce similarly appearing individuals. The local populations occupying distant parts of the range of a subspecies may therefore have very different heredity, even though the animals have the same general appearance.

The subspecies should, accordingly, in my opinion, be considered to be primarily an ecologic unit (Dice and

Blossom, 1937: 114-115). The members of a subspecies tend to occupy similar sorts of habitats, and at least some subspecific characters are known to be correlated with certain environmental features.

The taxonomy of subspecies must of necessity be based on morphological characters. This means that in mammals the color of the pelage and the dimensions of the body and its parts must form the basis of classification. The hereditary constitution of an animal or of a population, however, can not with our present knowledge be analyzed. Neither are we able to determine the ancestors of a subspecies except by comparison of its characters with those of other living subspecies. The fossil material available for most species is inadequate to give information about the evolution of subspecies. The subspecies as we recognize it in the field and in the museum therefore is composed of individuals of the same species which appear to be more or less similar in characters and which live in the same general area.

In regions of general environmental uniformity the subspecies may be expected to be more or less constant in characters, with local races poorly marked. In regions of considerable environmental diversity, on the contrary, the subspecies will likely be variable, with many local races, some of which may be strongly marked. Such variable subspecies are of course difficult to classify, especially when several opposing ecologic tendencies are involved.

The interpretation of a subspecies as being an ecologic trend is, it seems to me, more sound than the current concept of the vertebrate taxonomist, which holds that the subspecies is a unit of descent, and which implies that it also is a unit of heredity. There is good evidence that subspecies are not uniform in hereditary constitution and there also is good evidence for the polyphyletic origin of some subspecies. Accordingly, the concept that the subspecies results from an ecologic tendency more or less

uniformly expressed over a definite but not necessarily continuous area, seems most in accordance with the facts.

SUMMARY

Within every wide-ranging subspecies of animal there is a considerable amount of local variability, at least a considerable part of which is based on hereditary differences. The pelage color of *Peromyscus* and other small mammals tends to match the color of the surface soil of the habitat, demonstrating a control by the environment of part of the heredity of these animals. There also is evidence that some subspecies of *Peromyscus* have had a polyphyletic origin. Accordingly, the subspecies is considered to be primarily an ecologic unit, rather than a unit of similar descent or of similar heredity.

LITERATURE CITED

- Davis, W. B.
1938. *Jour. Mammalogy*, 19: 338-342.
- Dice, Lee R.
1937. *Univ. Mich. Occ. Pap. Mus. Zool.*, 352: 1-32, 1 map, 2 figs.
1938. *Univ. Mich. Occ. Pap. Mus. Zool.*, 375: 1-19, 1 map.
1939. *Univ. Mich. Contrib. Lab. Vert. Gen.*, 9: 1-16, 1 map.
1939. *Univ. Mich. Contrib. Lab. Vert. Gen.*, No. 12: 1-22, 1 map.
- Dice, Lee R. and Philip M. Blossom
1937. "Studies of Mammalian Ecology in Southwestern North America, with Special Attention to the Colors of Desert Mammals." Carnegie Inst. Wash., Publ. No. 485. iv + 125 pp., 8 pls. 8 figs.
- Merriam, C. Hart
1890. *N. Amer. Fauna* (U. S. Dept. Agr., Div. Ornith. and Mamm.), 3: 5-34.
- Murie, O. J. and Adolph Murie
1931. *Jour. Mammalogy*, 12: 200-209, 1 fig.
- Osgood, Wilfred H.
1909. *N. Amer. Fauna* (Bür. Biol. Surv.), 28: 1-285, 8 pls., 12 figs.
- Sumner, F. B.
1917. *AM. NAT.*, 51: 173-185, 1 fig.
1926. *Jour. Mammalogy*, 7: 149-184, 4 pls., 9 figs.
1932. *Biblio. Genetica*, 9: 1-106, 24 figs.
- Wright, Sewall
1932. *Proc. 6th Inter. Cong. Genetics*, 1: 356-366, 4 figs.

SPECIATION FROM THE POINT OF VIEW OF GENETICS^{1,2}

DR. M. R. IRWIN AND DR. R. W. CUMLEY

DEPARTMENT OF GENETICS, UNIVERSITY OF WISCONSIN

ONLY a very limited discussion will be possible, in the brief space of time at our disposal, on a small sector of the general subject of "Speciation from the Point of View of Genetics." Other symposia and various authors have dealt admirably with the influence of different aspects of genetics on the subject of speciation as a part of the larger field of evolution, and one might well question whether old ideas may be clothed in new words in such a manner as to make them worthy of presentation.

Ordinarily, we take for granted that the primary factors in the evolution of species are (a) gene mutation and (b) chromosome aberrations of the various kinds. Nevertheless, despite this assumed acceptance, in principle, of the basic rôle of gene mutation in speciation, questions have been raised by various authors as to whether the differences in heritable characters within a species (*i.e.*, differences due to the action of allelic genes) can also account for the differences between species. Arguments both pro and con have been advanced, from which we may conclude that additional experimental evidence is still needed. In this discussion, it is proposed to limit the remarks to certain aspects of the rôle of gene mutation in speciation, particularly as the genes affect the chemical composition of the blood cells. A part of the material to which reference will be made has not yet been published in detail.

¹ Read at a symposium on "The Relation of Genetics to Geographical Distribution and Speciation," before Section F—Zoological Sciences, American Association for the Advancement of Science, Milwaukee, Wisconsin, June 20, 1939.

² Paper from the Department of Genetics, Agricultural Experiment Station, No. 250. The investigations in this laboratory referred to in this paper have been supported in part by grants from the Rockefeller Foundation and from the Wisconsin Alumni Research Foundation.

We must admit that experimental analyses of genetic differences and similarities between species are relatively few, in either animals or plants. Even in species which hybridize and whose species-hybrid is relatively fertile, such studies meet with difficulties. Not the least of these difficulties is that of recognizing the effects of single genes apart from the particular complex in which they are found in one species or the other. There would be an advantage, then, in using in such studies the characters produced by genes whose effects are the same, no matter what other genes are present.

An example of this kind of character is that of the antigens of the red blood cells, in so far as they have been studied within any species. The assumption is that the action of the gene on its particular antigen is more or less direct. However, a few results have been obtained, in species crosses of doves (Irwin, 1932; Irwin and Cole, 1936) and in chickens (Thomsen, 1936), which imply complementary interaction of genes having effects on the antigens of the red blood cells. It hardly need be stated that these antigenic characters are as yet detectable only by the use of immunological reagents.

No other cellular antigens have been studied so extensively as those of the human blood cells, of which there are the two well-known systems. The first of these is comprised of the characters \bar{A} , \bar{B} and \bar{O} , which are produced by triple alleles. Both \bar{A} and \bar{B} are dominant to \bar{O} (in our opinion, this seeming recessiveness of the \bar{O} character is probably due to the lack of a readily available and potent reagent for this antigen), and both \bar{A} and \bar{B} are fully expressed when heterozygous. Another pair of characters, the \bar{M} and \bar{N} , are produced by a pair of alleles, independently inherited from those producing the \bar{A} and \bar{B} antigens. Analyses of the chemical composition of the \bar{A} and \bar{B} characters by different investigators indicate that they are complex nitrogenous polysaccharides.

It becomes a question of considerable interest as to

whether these cellular characters, presumably therefore their causative genes, are present in any of man's relatives. Tests to determine these relationships have already been performed by various workers, with results as given in Table I.

TABLE I*
HUMAN BLOOD-CELL CHARACTERS IN THE BLOODS OF APES AND MONKEYS

	O	A	B	AB	M	N	MN
Chimpanzees	+	+	-	-			(+)
Gorillas	-	+	-	-			
Orangs	-	+	+	+	(+)		
Gibbons	-	+	+	+	(+)		
Cercopithecidae (Old World species)	-	-	-	-	(+) [†]	-	
Platyrrhina (New World species)	-	-	(+)	-	(+) [‡]	-	
Lemuridae		(+) [§]	(+)		-	-	

* A part of this table is taken from Wiener (1939).

Symbols. A plus sign (+) indicates the presence of the particular antigen or antigens in the cells of the species; a dash (-) indicates that the character has not definitely been found; parentheses around the plus sign (+) indicate that a similar but not identical component to that in humans is present.

[†] In 7 species of 4 genera tested.

[‡] In only one species (White spider monkey, genus *Ateles*) of 6 species of 4 genera tested.

[§] Positive reactions were obtained with bloods of several species of lemurs, indicating the presence of a factor somewhat related to the \bar{A} of humans.

Considering first the characters \bar{A} , \bar{B} and \bar{O} , it has been found (Landsteiner and Miller, 1925a) that the particular antigens, when present alone or together in the blood of the anthropoid apes, are seemingly identical with those of human blood. On this basis it may be concluded that although we have no actual knowledge of the inheritance of the \bar{A} character, for example, in any of these species of apes, it is probable that the gene in each of these species is homologous to the one producing this substance in man.

However, when species of lower monkeys were analyzed (Landsteiner and Miller, 1925b) for the presence of the \bar{A} and \bar{B} antigenic characters of humans, it was noted that comparable blood characters were found only in the New World monkeys (Platyrrhina) and in the Lemuridae. Twelve species (22 individuals in all) taken from 5 genera of the Platyrrhina, and 6 species (8 individuals) of Lemuridae were tested by special reagents for the presence or absence of the \bar{A} and \bar{B} components. A character similar to, but not identical with the \bar{B} anti-

gen of humans was found in the cells of each of these species of the New World, and in the Lemuridae, while no trace of either the \bar{A} or \bar{B} antigens could be detected in the cells of 46 individuals of 18 species of Old World (Cercopithecidae) monkeys. (In the table, parentheses around the "+" sign indicate the presence of an antigen similar to, but not identical with, the particular character.)

Because of the wide-spread occurrence of the Forssman antigen, and a certain chemical relationship which the \bar{A} substance of humans has to it, it is somewhat surprising that there was no definite indication of a character related to the \bar{A} (of humans) in the Old and New World monkeys. As shown in Table I, an identical character appears in chimpanzees, gibbons, gorillas and oranges, and a related but not identical character is found in at least some of the species of lemurs. This might well be taken as evidence of the antiquity of the genes producing both the related and identical substances, the conclusion being that the genes for both \bar{A} and \bar{B} were probably present in a common ancestor of man and the higher apes. Also, since a gene for the \bar{B} -like character is found in the New World monkeys, and not in those of the Old World, and that for \bar{A} found infrequently, if ever, in those families, perhaps the forerunner of the gene for the \bar{B} -substance is the older of the two.

Similar studies (Landsteiner and Wiener, 1937; Wiener, 1938) on the distribution of the \bar{M} and \bar{N} antigens in some of the apes and lower monkeys have shown that no species of those tested contains a character identical with either the \bar{M} or \bar{N} substance of humans. There is, however, a comparable component in the cells of many species, as listed in Table I. This differentiation of the identical and comparable components is possible either by using several immune sera, or by the technic of antibody-absorption. Without the results following agglutinin-absorption it would be assumed that the \bar{MN}^3 com-

³ Tests on twelve chimpanzees have shown that the combination of the \bar{MN} -like components was found in each individual, this combination paralleling the heterozygote (\bar{MN}) which occurs in humans in about 50 per cent.

bination in chimpanzees and the \bar{M} -like characters in orangs, gibbons, and wherever found in other species, were identical with the \bar{M} or \bar{N} characters of humans. The inference from this kind of evidence would be that the same gene was present in all of these species.

The actual results show very clearly that the \bar{M} -like antigen in the different species, although related, is not identical in chemical composition with the \bar{M} character of human cells. Presumably, then, the respective genes producing the \bar{M} -like character in these several species are likewise related to, but not identical with, the gene for the \bar{M} -substance of humans. (The tests made by the workers cited above suggest differences in the M -properties of the cells of the various species of monkeys in which such properties are present. If more critical tests were performed in this respect, it is probable that the \bar{M} -like character would be found not to be identical in more than a few of these species, if in any.) This explanation would apply also to the genes producing the \bar{B} -like characters of the Platyrrhina and the lemurs. An alternative explanation would be that the same gene interacting with the different protoplasts of the several species would give a related but different end-product. On the other hand, the fact that the \bar{A} and \bar{B} antigens of humans are identical with characters found in the anthropoids, singly or together, would weaken the alternative proposal.

Let us assume, then, that a gene with an antigenic effect existed in a common ancestor of these different species. It would be reasonable to conclude that, during the evolution of the various species, this gene must have changed in different ways in those different species, so

of the population. One might assume a single gene in the chimpanzee with an effect related to two different antigens in another species (humans). This, however, seems somewhat improbable. It would appear that, unless these characters are found separately in other chimpanzees, there is in this species an instance of genes with contrasting effects always occurring together, presumably being on the same chromosome, whereas the genes in humans related to each of these are alleles. Possibly the explanation for the bar-eye effect in *Drosophila* would apply here.

that its effects, while similar, are not identical. We can only speculate as to whether this particular gene in each of these species is an allelic relation to that of the humans. The decreasing degree of similarity noted (*loc. cit.*) between some of the species for both the \bar{B} -like and \bar{M} -like antigens would suggest also that there are different degrees of relationship in the genes involved, among themselves, and to those in man.

From this and other evidence, we may conclude that there probably are three categories of genes which make for resemblances and differences between related species. In the first class there are those genes of the two species which are homologous, and which produce the same effects. In the next class are genes which are related but not identical, and which produce similar but not identical effects. (Naturally, if the relationship of this class of genes, one to the other, was that of one allele to another, although found in different species, this category would be superfluous.) Finally, in the third category there are those genes which are not alike and which make for the differences that exist between one species and another. Presumably, we would expect that the relative relationship between species would depend upon the proportion of their respective genes that were shared, in contrast with those that were specific for either species.

If within different species there were many genes with effects upon the antigens of the red blood cells, it would be anticipated that an immunological distinction between the cells of any two species could be readily accomplished. Such a comparison is shown in Fig. 1 for the two species of doves, Pearlneck (*Streptopelia chinensis*) and Ring Dove (*St. risoria*). It will be noted that each species shares a part of its cellular pattern with the other and, in addition, each has a part which is peculiar to itself. (The proportions in the diagram have of necessity been set arbitrarily.) Further, the species hybrid contains all of the properties common to both parents, nearly all of the species specific properties of each, and one or more characters not found in either parent.

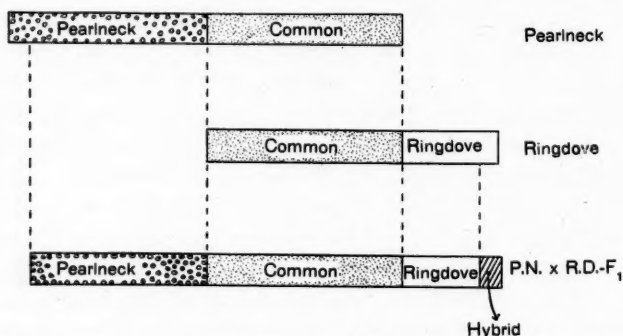


FIG. 1. A diagram of the comparison of the antigenic composition of the cells of Pearlnecks, Ring doves and the F_1 hybrids.

These characters peculiar to the hybrid are of interest because either the same or related substances are normally found in a few other species. Presumably, then, certain of the genes, which by their interaction in the hybrid produce the hybrid components, are a part of the normal genic complex of other species. The production of these "hybrid components" does not seem to be an attribute of all species hybrids. In only two of the seven different species hybrids in doves tested to date has there been definite evidence of a "new" or "hybrid" substance. Other than these components, the relationship of each of the different species hybrids to the common and specific components of the two parental species is approximately as pictured for the hybrid between Pearlneck and Ring Dove.

Following continued backcrosses to the Ring Dove, a separation of the specific Pearlneck components has been observed (Irwin, 1939). Ten distinct major Pearlneck characters have been isolated so that representatives of any single character, when mated to Ring Doves, produce offspring of which approximately half contain the particular character and half do not. This evidence, combined with that from other sources, practically establishes the veracity of the statement that the antigens of the red blood cells are gene-determined. Comparisons of

the cellular antigens of different species are then somewhat more than an indirect way of measuring the gross gene relationships of the species.

Utilizing as testers the unit-antigens of Pearlneck, it has been found that Pearlneck possesses in common with other related species, and in varying combinations, certain of the antigens not shared with Ring Dove. What then from these studies as a whole can we say concerning the genic complex of a single species in relation to a number of other species? Does each species have particular genes which set it apart from all others? Or is a species simply a different combination of a given number of genes, all of which might be present if the genes of two or more other species were combined?

An absolute answer to these alternative questions can not be given at present. However, rather exhaustive tests on the antigenic composition of two species, Pearlneck and *Columba guinea*, and less exhaustive tests on several other species of pigeons and doves, entirely substantiate the proposal that each species possesses certain genes with antigenic effects not found at all in other species. The remainder of the antigenic pattern of the species is shared, in many different combinations, with other related species, presenting a most intricate pattern of species relationships.

An interesting point has been noted as the result of comparisons of the cellular substances of the different species of pigeons (*Columba*) carried out in our laboratory. We have made extensive tests of the inter-relationships of five species of Old World and six species of the New World pigeons,⁴ which in summary suggest a correlation of relationship with habitat in the two hemispheres.

Briefly, as may be noted in Fig. 2, there appear to be antigens which are common to species of both the Old and

⁴ The species of pigeons of the Old World are *Columba guinea*, *C. livia domestica*, *C. janthina*, *C. oenas* and *C. palumbus*. Those of the New World, *C. fasciata*, *C. flavirostris*, *C. leucocephala*, *C. maculosa*, *C. picazuro* and *C. rufina*.

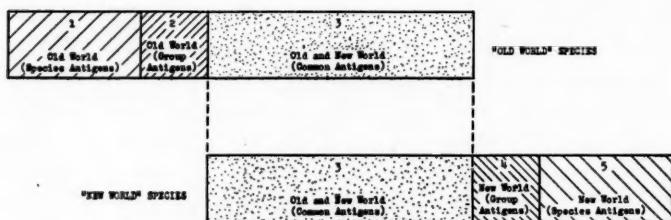


FIG. 2. Interrelationships of antigens of Old and New World species of the genus *Columba*.

1. Antigens of Old World species of *Columba*, including those characteristic of each species.
2. Antigens of Old World species of *Columba*, contained in many if not in all Old World species.
3. Antigens shared by both Old and New World species of *Columba*.
4. Antigens of New World species of *Columba*, contained in many if not in all New World species.
5. Antigens of New World species of *Columba*, including those characteristic of each species.

the New World. Further, within the species of the Old World there are other antigens which set these species apart as a group from any of those of the New World. These components are shared by many, if not by all, of the Old World species. And then there are other antigens which set each species apart from every other species of the Old World. Likewise, the species of the New World have a group of cellular characters which are not found in those of the Old World, and which are present in most, if not in all, of the species of the New World. Also, each species has its own distinctive antigens, as stated above.

As a corollary, we may say that by these tests, and for these species, we have found that any species of pigeon of the New World is more similar to any other species of the New World than it is to any Old World species. Likewise, any species of the Old World is more like any other pigeon of the Old World than is any species of the New World.

A very few exceptions to these general relationships have been observed, and more may become apparent when and if representatives of other species of pigeons

are available for inclusion in these tests. However, these exceptions do not, in our opinion, detract from the authenticity of the more or less sharp differentiation of the species from the Old and New World, respectively.

At the present time, it seems that these analytical procedures may eventually enable us to fit the many species of pigeons and doves into a phylogenetic pattern, to which it is our hope that a genetic explanation can be applied.

LITERATURE CITED

- Irwin, M. R.
1932. *Proc. Soc. Exp. Biol. and Med.*, 29: 850-851.
1939. *Genetics*, 24: 709-721.
- Irwin, M. R., and L. J. Cole
1936. *Jour. Exp. Zool.*, 73: 309-318.
- Landsteiner, K., and C. Philip Miller, Jr.
1925a. *Jour. Exp. Med.*, 42: 853-862.
1925b. *Ibid.*, 42: 863-872.
- Landsteiner, K., and A. S. Wiener
1937. *Jour. Immunol.*, 33: 19-25.
- Thomsen, O.
1936. *Hereditas*, 22: 129-144.
- Wiener, A. S.
1939. "Blood Groups and Blood Transfusion." Charles C Thomas:
Springfield, Illinois.
1938. *Jour. Immunol.*, 34: 11-18.

BREEDING STRUCTURE OF POPULATIONS IN RELATION TO SPECIATION¹

PROFESSOR SEWALL WRIGHT

THE UNIVERSITY OF CHICAGO

INTRODUCTION

THE problem of speciation involves both the processes by which populations split into non-interbreeding groups and those by which single populations change their characteristics in time, thus leading to divergence of previously isolated groups.

The first step in applying genetics to the problem is undoubtedly the discovery of the actual nature of the genetic differences among allied subspecies, species and genera in a large number of representative cases. Differences which tend to prevent cross-breeding are obviously especially likely to throw light on the process of speciation, but all differences are important.

Our information here is still very fragmentary. We know enough, however, to be able to say that there is no one rule either with respect to cross-sterility or to other characters. In some cases the most significant differences seem to be in chromosome number and organization. At the other extreme are groups of species among which gross chromosome differences and even major Mendelian differences are lacking, both cross-sterility and character differentiation depending on a multiplicity of minor gene effects. In general, there are differences at all levels (*cf.* Dobzhansky, 1937).

But even if we had a complete account of the genetic differences within a group of allied species, we would not necessarily have much understanding of the process by which the situation had been arrived at. A single mutation is not a new species, except perhaps in the case of polyploidy. The symmetry of the Mendelian mechanism

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is such that any gene or chromosomal type tends to remain at the same frequency in a population except as this frequency is changed either by some steady evolutionary pressure (such as that due to *recurrent* mutation, to various kinds of selection, to immigration and to differential emigration) or by the accidents of sampling, if the number of individuals is small. The elementary evolutionary process, from this view-point, is change of gene frequency.

It is to be expected that the nature of the process will be found to be affected by what I have called the breeding structure of the species, and it is this aspect of the matter that I wish to discuss here. Such a discussion involves at least three steps. First, there is the observational problem of determining what the breeding structures of representative species actually are. Naturalists are only beginning to collect the detailed information which turns out to be necessary, but that which we have indicates situations of great complexity. The second step is that of constructing a mathematical model which represents adequately the essential features of the actual situation while disregarding all unimportant complications. The third step is the determination of the evolutionary implications of a given breeding structure in relation to mutation and selection. As difficult problems of description and mathematical formulation are also involved in the cases of mutation and selection pressures, the whole problem is exceedingly complex. I can only discuss the implications of certain very simple models of breeding structure, chosen partly because they appear to correspond to situations which one might expect to find in nature, but partly also because of mathematical convenience.

EVOLUTION UNDER PANMIXIA

The simplest situation, under biparental reproduction, is that of a large population, breeding wholly at random (panmixia). If sufficiently large, variability due to accidents of sampling is negligible. Each gene frequency

shifts steadily under the pressures of selection and recurrent mutation. Mathematical formulations of these pressures have been given. Letting q be the frequency of a given gene, $(1-q)$ that of its alleles, u and v the mutation rates respectively from and to the gene in question and \bar{W} the mean selective value of all possible genotypes, weighted by their frequencies, the change in gene frequency in a generation is given by the following formula (Wright, 1937):

$$\Delta q = v(1-q) - uq + \frac{q(1-q)s\bar{W}}{2N\Delta q}$$

For a gene which causes the same difference from its allele in all combinations and which lacks dominance, the term for selection pressure reduces approximately to $sq(1-q)$, where s is the selective advantage over the allele.

The numbers of generations necessary for any given shift in gene frequency, under various hypotheses, have been presented by Haldane (1932 and earlier). This sort of process has been taken as typical of evolutionary change by R. A. Fisher (1930), who has compared its unswerving regularity to that of increase in entropy in a physical system.

If, however, conditions are constant, this process comes to an end at an equilibrium point at which opposing pressures balance each other ($\Delta q = 0$). At this point there is stability of the species type in spite of continual occurrence of mutations, an extensive field of variability and continuous action of selection. On the other hand, conditions never are wholly constant. It is possible that evolution, in each series of alleles, may consist of an unswerving pursuit of an equilibrium point, which is itself continually on the move because of changing conditions.

The postulate that variations in gene frequency, due to accidents of sampling, are negligible calls for some comment. The variance in one generation is $\sigma^2_{\Delta q} = \frac{q(1-q)}{2N}$ in a diploid population of effective size N . This is cumu-

lative and may cause wide divergence from equilibrium if the population is not too large. The systematic evolutionary pressures directed toward equilibrium and this sampling variance determine between them a certain distribution of values of the gene frequency instead of a single equilibrium point. The general formula can be written as follows (Wright, 1937):

$$\varphi(q) = (C/\sigma^2_{\Delta q}) e^{\int (\Delta q / \sigma^2_{\Delta q}) dq}$$

For the values of Δq and $\sigma^2_{\Delta q}$ given above this reduces to

$$\varphi(q) = C \bar{W}^{2N} q^{4Nu-1} (1-q)^{4Nv-1}$$

In the special case of no factor interaction and no dominance, the term \bar{W}^{2N} becomes approximately $e^{4Ns q}$. There is a marked tendency toward chance fixation of one allele or another if $4Ns$, $4Nv$ and $4Nu$ are all less than 1 while such variability is negligible if these quantities are large (e.g., as large as 100).

The possible evolutionary significance of these random variations in gene frequency in a panmictic population has been considered elsewhere (Wright, 1931, 1932) and will not be discussed further here.

Mating never is wholly at random. It is important to determine whether departures from panmixia have significant effects on the evolutionary process and if so whether these consist merely in impeding the pursuit of equilibrium or whether they may not bring about progress of a different sort.

One limitation on the effectiveness of selection in a panmictic population is that it can apply only to the *net effects* in each series of alleles. It is really the organism as a whole that is well or ill adapted. A really effective selection pressure should relate to genotypes not genes. But in a panmictic population, combinations are formed in one generation only to be broken up in the next.

If a selective value (W) is assigned to every one of the practically infinite number of possible combinations of genes of all loci, the array of such values forms a surface in a space of at least as many dimensions as there are loci, more if there are multiple alleles. Because of non-

additive factor interactions, this surface in general has innumerable distinct peaks (*i.e.*, harmonious combinations) each surrounded by numerous closely related but slightly less adaptive combinations and separated from the others by valleys. Selection according to net effect can only carry the species up the gradient to the nearest peak but will not permit it to find its way across a valley to a higher peak. Evolution would have a richer field of possibilities under a breeding system that permitted exploration of neighboring regions in the surface of adaptive values, even at some expense in momentary adaptation.

A somewhat similar situation holds within systems of *multiple alleles* (*cf.* Timoféeff-Ressovsky, 1932). There is presumably a limit to the number of alleles that can arise from a given type gene by a single act of mutation. But each of these mutations presumably can give rise to mutations at two steps removed from the original type gene and so on in an indefinitely extended network. If there is approximate fixation of one allele (to be expected in general under panmixia), only those mutations that are at one or two removes have any appreciable chance of occurrence. There will be continual recurrence of the same mutations without real novelty. A breeding system that tolerates a continually shifting array of multiple alleles in each series in portions of the population, gives the opportunity for a trying out of wholly novel mutations which occasionally may be of great value. The question then is whether there are breeding structures that permit trial and error both within each system of multiple alleles, and within the field of gene combinations, in such a way as to give a richer field of possibilities than under the univalent determinative process in a panmictic population.

EVOLUTION UNDER UNIPARENTAL REPRODUCTION

At the opposite extreme from the system of random mating is that in which there is uniparental reproduction.

Under vegetative multiplication, or under diploid parthenogenesis, each individual produces a clone in which all individuals are of exactly the same genotype, except for occasional mutations. Continued self fertilization also leads to the production of groups of essential identical individuals.

Suppose that a highly variable panmictic population suddenly shifts to uniparental reproduction. Selection then would be between genotypes. Those combinations that are most adaptive would increase, including perhaps rare types that would have been broken up and lost under panmixia. The less adaptive combinations would soon be displaced. Selection would be exceedingly effective until only one clone was left in each ecological niche. But at this point evolution would come to an end, except for the exceedingly rare occurrence of favorable mutations.

It is obvious that a certain combination of the preceding systems should be much more effective than either by itself (*cf.* Wright, 1931). Prevailing uniparental reproduction, with occasional crossing would permit an effective selection by genotypes to operate in a continually restored field of variability. This combination is of course one that has been used most effectively by plant breeders. It is found in many plants and animals in nature and has presumably been an important factor in their evolution.

The demonstration of the evolutionary advantages of an alternation of periods of uniparental reproduction with cross-breeding may seem to prove too much, since it is not usual in those groups that are usually considered to have evolved the most, the higher arthropods and vertebrates. Perhaps, however, there are other systems which also bring about differentiation of types and thus a basis for selection based on type rather than mere net gene effect, and which have more stability than arrays of clones.

EVOLUTION IN SUBDIVIDED POPULATIONS

A breeding structure that happens to be very conveni-

ent from the mathematical standpoint is one in which the species is subdivided into numerous small local populations which largely breed within themselves but receive a small proportion of their population in each generation from migrants which can be treated as random samples from the species as a whole. The basis for the partial isolation may be geographical, or ecological or temporal (breeding season). In the latter two cases an adaptive difference is postulated. We are not here considering the origin of this but rather its consequences on other characters.

Whatever the mechanism of isolation, its evolutionary significance can be evaluated in terms of the effective size of population (N) of the isolated group, the effective rate (m) of exchange of individuals between the group (gene frequency q) and the species as a whole (gene frequency q_t) and the local selection coefficient. It will be convenient here to write s for the net selection coefficient and to ignore mutation pressure (Wright, 1931).

$$\Delta q = sq(1-q) - m(q - q_t)$$

If s in a local population is much larger than m , we have approximately

$$\hat{q} = 1 - \frac{1}{s} [m(1 - q_t)] \quad \text{if } s \text{ is positive}$$

$$\hat{q} = \frac{mq_t}{(-s)} \quad \text{if } s \text{ is negative}$$

If the values of s among local populations show differences greater than m , there will be marked adaptive differentiation of such populations. There is an approach toward fixation of the locally favored gene largely irrespective of the frequency in the species as a whole.

The importance of isolation in evolution seems to have been urged first by M. Wagner as permitting divergent evolution under the control of different environments. Wagner thought of environment as directly guiding the course of evolutionary change, when its effects were not swamped by those of cross-breeding. A similar view has been held by many others since his time who have considered such orderly clines among geographical races as

those described by the laws of Bergmann, Gloger, and Allen. While direct control over mutation is not in line with present knowledge of genetics, indirect control through differential selection seems probable enough in these cases (*cf.* Dobzhansky, 1937; Huxley, 1939).

Davenport (1903) and Goldschmidt (1934) have stressed the likelihood of the spreading of the range of species by the diffusion of preadaptive mutations into territories in which they are isolated from the first by the inability of the typical members of the species to live. Goldschmidt has interpreted the major differences among races of *Lymantria dispar* in this way. He finds these differences primarily in such physiological characters as developmental rate, length of diapause, etc. Mathematically, this would be a special case of the foregoing scheme.

Differential selection has been considered so far as a factor making only for divergence of groups within the species and thus tending toward splitting of the latter. There is a possibility, however, that it may be a factor making for progressive evolution of the species as a unit. Particular local populations may, by a tortuous route, arrive at adaptations that turn out to have general, instead of merely local, value and which thus may tend to displace all other local strains by *intergroup* selection (excess emigration). In terms of our multidimensional surface of adaptive values, a particular substrain may be guided from one peak to another by a circuitous route around a valley which would probably not have been found except by such a trial and error mechanism. As different alleles may approach fixation in different populations, mutations at two or more removes from the original type have more opportunity for occurrence than if the population were homogeneous. Thus there may be trial and error within series of alleles as well as between gene combinations.

Let us now turn to the case in which the local selection coefficient is smaller instead of larger than m . The local equilibrium frequency (\hat{q}) is approximately as follows.

$$\hat{q} = q_t + \frac{sq_t}{m} (1 - q_t)$$

The values in different local populations in which s is smaller than m are clustered closely about the mean gene frequency, q_t . Selection causes no important differentiation. There may however be variability of each local population due to accidents of sampling if N is small and, consequently, much non-adaptive differentiation among such populations at any given moment.

$$\varphi(q) = Ce^{4Nsq} q^{4Nm q_t - 1} (1-q)^{4Nm(1-q_t) - 1}$$

Figure 1 shows the form of the distribution for various values of Nm , taking $q_t = \frac{1}{2}$ and assuming no selection ($s = 0$). The variance in this case is as follows.

$$\sigma^2 q = \frac{q_t(1-q_t)}{4Nm+1}$$

The distribution of gene frequencies is U shaped, implying random drifting from fixation in one phase to another if m is less than $\frac{1}{4Nq_t}$ and $\frac{1}{4N(1-q_t)}$. This again would permit trial within each series of alleles, and also between gene combinations.

The latter at least would be important even with larger values of m relative to $\frac{1}{4}N$. With $Nm = 5$, the standard deviation of values of q is 22 per cent. of its limiting value $\sqrt{q(1-q)}$. Such variability tends to become unimportant however if Nm is much larger.

Gulick seems to have been the first to point out the possible significance of isolation in bringing about a non-adaptive differentiation of local races. He has been followed by others, notably recently by Kinsey in his studies of the gall wasps of the genus *Cynips* (1929, 1936). A study of eleven isolated mountain forests in the Death Valley region by Dobzhansky and Queal (1938) showed a close approach to random mating with no appreciable selection within localities. Between localities on the other hand, frequencies ranged from 51 per cent. to 88 per cent., 2 per cent. to 20 per cent., 8 per cent. to 39 per cent. with standard deviations which can be accounted for by an effective value of Nm of about 5.1. The much greater standard deviation for the range of *D. pseudoobscura* as a whole shows that this differentiation is cumulative with distance.

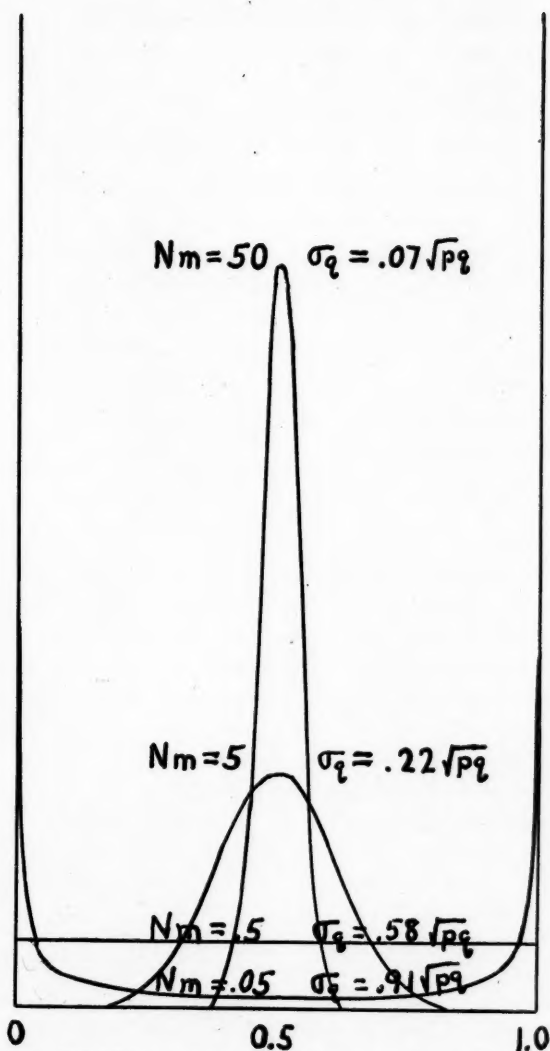


FIG. 1. The distribution of gene frequencies for various values of Nm , taking $q_1 = \frac{1}{2}$ and assuming no selection. The symbol p is used for $1-q$.

EFFECTIVE SIZE OF POPULATION

There appears to be the difficulty here that the number of individuals in such a form as *Drosophila* is so enor-

mous that it is difficult to conceive of a limitation in numbers as having any appreciable sampling effects. However, the effective N may be very much smaller than the apparent N (Wright, 1938).

If the number of the two sexes (N_m males, N_f females) is unequal, it can be shown that effective $N = \frac{4N_m N_f}{N_m + N_f}$. With unequal numbers, the effective size of population depends more on the smaller number than on the larger number. Thus with N_m males but an indefinitely large number of females, $N = 4N_m$.

Again, different parents may produce widely different numbers of young. If σ^2_κ is the variance in number of gametes contributed by individuals to the following generation in a population (N_0) that is maintaining the same numbers ($\bar{\kappa} = 2$), $\sigma^2_\kappa = \frac{\sum(\kappa - 2)^2}{N_0}$

$$N = \frac{4N_0 - 2}{2 + \sigma^2_\kappa}$$

The effective size of population is twice as great as the apparent in the highly artificial case in which each parent contributes just two gametes. Effective and apparent size of population are the same if the number of gametes contributed by different parents vary at random (Poisson distribution). If, as would often be the case, most of the offspring come from a small percentage of the mature individuals of the parental generation, the effective size would be much less than the apparent size.

A population may vary tremendously in numbers from generation to generation. If there is a regular cycle of a few generations ($N_1, N_2 \dots N_n$) an approximately equivalent constant population number can be found.

$$N = \frac{n}{\sum_{x=1}^n [1/N_x]}$$

This is controlled much more by the smaller than by the larger numbers. Thus if the breeding population in an isolated region increases ten-fold in each of six generations during the summer (N_0 to $10^6 N_0$) but falls at the

end of winter to the same value, N_0 , the effective size of population ($N = 6.3N_0$) is relatively small.

In such a cycle, certain individuals in favorable locations are likely to start reproduction earlier than others, perhaps getting a start of a whole generation. In a rapidly breeding form, these few individuals would contribute overwhelmingly more than the average to all later generations. Thus, by a combination of the two preceding principles, the effective size of population may be very small indeed.

The possible evolutionary significance of periodic reduction in the size of natural populations has been discussed by a number of authors. Elton (1934) especially has maintained that chance deviations in the characteristics of survivors at the time of least numbers may have important effects of this sort.

An important case arises where local populations are liable to frequent extinction, with restoration from the progeny of a few stray immigrants. In such regions the line of continuity of large populations may have passed repeatedly through extremely small numbers even though the species has at all times included countless millions of individuals in its range as a whole (*cf.* Fig. 2).

Such mutations as reciprocal translocations that are very strongly selected against until half fixed seem to require some such mechanism to become established. There is an exceedingly deep valley in the surface \bar{W} representing the mean adaptive value in populations with given frequencies of old and new chromosomes, and the term \bar{W}^{2N} in the formula for the joint chromosome frequencies is so small, where N consists of more than some half-dozen individuals that fixation is virtually impossible. Yet translocations have been noted between *Drosophila* species (*e.g.*, *D. pseudoobscura* and *D. miranda*, Dobzhansky and Tan, 1936) although they are far less common than inversions. The difficulty referred to here does not, of course, apply in species that reproduce vegetatively or by self-fertilization.

We have discussed various considerations that make

effective N much smaller than at first apparent. The effective amount of cross-breeding may also be much less than the actual amount of migration seems to imply. Most of the immigrants are likely to come from neighboring groups, differing less from the receiving population in gene frequency than would a random sample from the

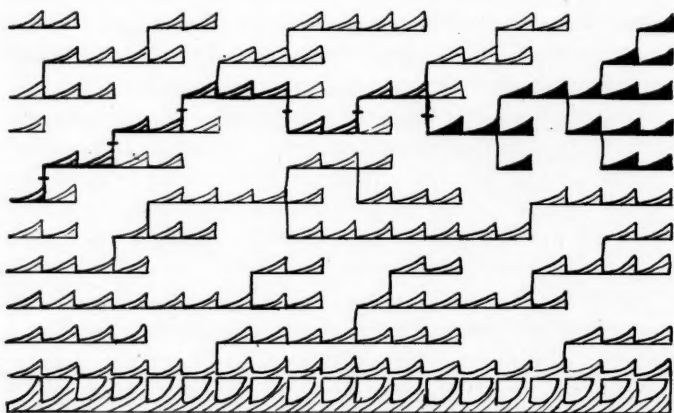


FIG. 2. Diagram of breeding structure in a species in which the populations in certain regions are liable to frequent extinction with reestablishment by rare migrants. Different territories are distinguished vertically. Generations proceed from left to right horizontally. The heavily shaded group represents a large population the entire ancestry of which has passed through small groups of migrants six times in the period shown.

species. If there is a correlation, r , between immigrants and receiving group, the m of the formula must be replaced by $m(1-r)$ if m is to continue to be the actual amount of replacement by immigration.

In the case of *Drosophila pseudoobscura*, it has been noted that Dobzhansky and Queal (1938) found variability in gene frequency among mountain forests of the Death Valley region which implied an effective value of Nm of about 5. For the species as a whole, variability is such that effective Nm must be only about one tenth as large as this (0.5).

ISOLATION BY DISTANCE

This last case leads to another model of breeding struc-

ture which may be of considerable importance (Wright, 1938). Suppose that a population is distributed uniformly over a large territory but that the parents of any given individual are drawn from a small surrounding region (average distance D , effective population N). How much local differentiation is possible merely from accidents of sampling? Obviously the grandparents were drawn from a larger territory (average distance $\sqrt{2} D$, effective population $2N$). The ancestors of generation n came from an average distance $\sqrt{n} D$ and from a population of average size nN . It is assumed that the variance of the ancestral range, either in latitude or in longitude, increases directly with the number of generations of ancestry.

Fig. 3 shows how the standard deviation of gene frequencies for unit territories of various effective sizes increases with distance. If $\sigma_q = .577\sqrt{q_i(1-q_i)}$ and $q_i = 1 - q_t = \frac{1}{2}$ all values of gene frequency are equally numerous ($\phi(q) = 1$). Any larger value implies a tendency toward fixation of one or the other allele in different local populations.

If the parents are drawn from local populations of effective size greater than 1,000, the situation differs little from panmixia even over enormous areas. There is considerable fluctuating local differentiation of unit territories where their effective size is of the order of 100, but not much differentiation of large regions unless effective N is much less.

Kinsey's (1929) description of the gall wasp, *Cynips pezomachoides erinacei*, conforms fairly well to the above model for the case of moderately large N . This subspecies ranges over some 500,000 square miles in north-eastern United States. Both the insects and their galls may differ markedly and consistently in collections taken from different trees or small groves at short distances apart, but the same variability is found throughout the range. There is little regional differentiation in this enormous territory, although at still greater distances

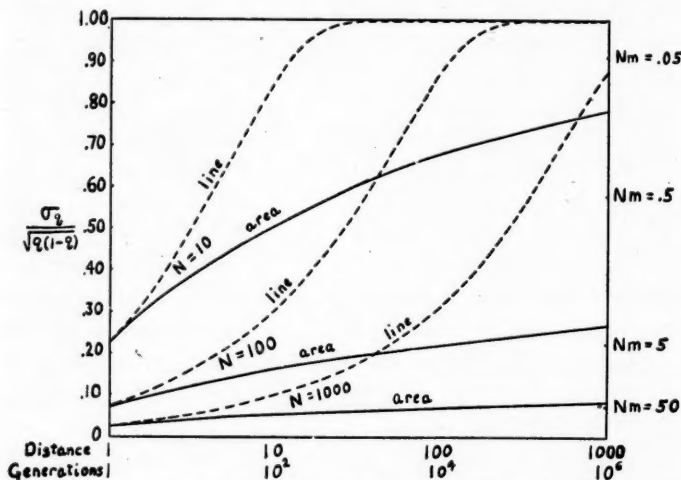


FIG. 3. The standard deviation of the mean gene frequencies of unit random breeding territories ($N = 10$; $N = 100$; $N = 1000$), in relation to mean distance. The case in which the population is distributed uniformly over an area is represented in solid lines, that in which it is distributed along one dimension by broken lines.

the species complex *C. pezomachoides* is subdivided into eight intergrading species.

In a species whose range is essentially one-dimensional (shore line, river, etc.) the ancestors of generation n come from an average distance of $\sqrt{n} D$ as before, but the effective size of population is $\sqrt{n} N$ instead of nN . Differentiation increases much more rapidly with distance than in the preceding case. This principle was suggested in qualitative terms by Thompson (1931) in his study of differentiation within species of river fish in relation to water distance. In weak swimmers (e.g., Johnny Darters) there was marked increase in average difference in number of fin rays with increased distance in spite of a continuous distribution. The differentiation with distance was not as rapid, however, as that in several species with discontinuous distribution (restricted to the smallest stream). On the other hand the strong swimmers of the rivers showed little or no differentiation throughout their entire ranges.

Such uniformity in breeding structure as implied above is not likely to be closely approximated in nature. Even where there is apparent continuity of a population, it is likely that conditions vary from place to place in such a way that there is excess multiplication at certain centers separated by regions in which the species would be unable to maintain itself permanently were it not for immigration (as in the breeding structure of Figure 2). Moreover, even with complete uniformity of conditions, local differentiation should result in the accidental attainment of more adaptive complexes in some regions than in others. As before, incipient nonadaptive differentiation may lead to a more important adaptive differentiation. The centers in which population is increasing most rapidly will become increasingly isolated from each other by the mere fact that they are centers of emigration.

A process of this sort has been postulated by Sumner (1932) in the case of subspecies of *Peromyscus*. Within subspecies, he found statistical differentiation of most local populations which may well have been of the type due merely to distance. But at the subspecies boundaries there was typically a zone of relatively rapid change. These boundaries were not necessarily along natural barriers to migration. Sumner compared them with the distributions which would result "if a collection of spherical rubber bags were placed in rigid containers and then strongly but unequally inflated."

The breeding structure of natural populations thus is likely to be intermediate between the model of subdivision into partially isolated territories and that of local inbreeding in a continuous population. In so far as it is continuous, it is likely to be intermediate between area continuity and linear continuity.

Summing up, we have attempted to show that the breeding structure of populations has a number of important consequences with respect to speciation. Partial isolation of local populations, even if merely by distance is important, not only as a possible precursor of splitting of the species, but also as leading to more rapid evolu-

tionary change of the population as a single system and thus more rapid differentiation from other populations from which it is completely isolated. Local differentiation within a species, based either on the nonadaptive inbreeding effect or on local conditions of selection or both, permits trial and error both within series of multiple alleles and between gene combinations and thus a more effective process of selection than possible in a purely panmictic population.

LITERATURE CITED

- Davenport, C. B.
1903. *The Decennial Publications*, 10: 157-176. The University of Chicago.
- Dobzhansky, Th.
1937. "Genetics and the Origin of Species." New York: Columbia University Press, 364 pp.
- Dobzhansky, Th., and M. L. Queal
1938. *Genetics*, 23: 239-251.
- Dobzhansky, Th., and C. C. Tan
1936. *Zeit. Ind. Abst. Ver.*, 72: 88-114.
- Elton, C. S.
1924. *Brit. Jour. Exp. Biol.*, 3: 119-163.
- Fisher, R. A.
1930. "The Genetical Theory of Natural Selection." Oxford: Clarendon Press, 272 pp.
- Goldschmidt, R.
1934. "Lymantria," *Bibliographia Genetica*, 11: 1-186.
- Haldane, J. B. S.
1932. "The Causes of Evolution." London: Harper and Bros., 235 pp.
- Huxley, J. S.
1939. "Bijdragen tot de dierkunde," pp. 491-520. Leiden: E. J. Brill.
- Kinsey, A. C.
1929. Studies No. 84, 85, 86. Indiana University Studies, Vol. 16.
1936. Indiana Univ. Publ., Science Series No. 4.
- Sumner, F. B.
1932. *Bibliographia Genetica*, 9: 1-106.
- Thompson, D. H.
1931. *Trans. Ill. State Acad. Sci.*, 23: 276-281.
- Timoféeff-Ressovsky, N. W.
1932. *Proc. 6th Internat. Cong. Genetics*, 1: 308-330.
- Wright, S.
1921. *Genetics*, 6: 111-178.
1922. *Bull. no. 1121*, U. S. Dept. of Agr., 59 pp.
1931. *Genetics*, 16: 97-159.
1932. *Proc. 6th Internat. Cong. Genetics*, 1: 356-366.
1937. *Proc. Nat. Acad. Sci.*, 23: 307-320.
1938. *Science*, 87: 430-431.

SPECIATION PHENOMENA IN BIRDS¹

DR. ERNST MAYR

AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK

EVOLUTION is a very complicated and many-sided process. Every single branch of biology contributes its share of new ideas and new evidence, but no single discipline can hope to find all the answers or is justified to make sweeping generalizations that are based only on the evidence of its particular restricted field. This is true for cytology and genetics, for ecology and biogeography, for paleontology and taxonomy. All these branches must cooperate and the worker in each field must try to apply an approach to the problems of evolution that is particularly suitable to the methods of his special field. It is obvious that the taxonomist will not find out very much about the origin of new genetic characters nor about their transmission from one generation to the next. On the other hand, the taxonomist will be able to give answers to certain questions which are not attainable by the geneticist since speciation is not a purely genetic process. To-day I shall try to discuss, as taxonomist and zoogeographer, some such questions relating to speciation in birds.

SPECIATION PHENOMENA IN BIRDS

Birds are a peculiar field for the study of speciation phenomena; in some ways they are particularly well suited for such studies and in other ways they are quite unsuitable. They are unsuitable, because the experimental genetic work is difficult and yields only meager results. The reason for this is that most wild birds are very difficult to breed; secondly, the sequence of generations is very slow (usually only one per year), and the number of offspring small; the number of chromosomes

¹ Read at a joint symposium on "Speciation" of the American Society of Zoologists and the Genetics Society of America, American Association for the Advancement of Science, Columbus, Ohio, December 28, 1939.

is very large and nearly every character that has been carefully examined is determined by a whole bevy of modifying genes.

To offset these disadvantages there are a number of unusual advantages. The principal one is that birds are better known taxonomically and biologically than any other group of animals. It is estimated that less than 100 species of birds remain undiscovered in the entire world, among an estimated total of 8,500 species, that is, about 1 per cent. (Mayr, 1935). In the more thoroughly investigated regions of the world (N. America, Europe) not a single new good species has been discovered in more than forty years. About three good species of birds are discovered annually in the entire world by numerous collecting parties and several score of working taxonomists. This amounts to an annual addition of 1/30 per cent. to the known number of species. The total number of valid subspecies and geographical races which are being described annually is about 200, or $\frac{3}{4}$ per cent. of the known 26,000 species or subspecies. Other groups of animals are very much less known. In the Cynipidae (gall wasps), for example, one single collector (Kinsey) added during the course of two seasons of field work no less than 36 species to the known 50 species of one genus, an addition of 72 per cent.

But in birds not only most of the forms are known, but also their exact geographical distribution and their variation. In fact, most taxonomic work on birds during the last fifty years has been devoted to the subdivisions of the species, the geographical races or subspecies. The methods and aims of this field closely approach those of the student of the genetics of populations, and it is no wonder that a close understanding between taxonomist and geneticist has developed in recent years.

SPECIES DEFINITION

"Speciation or species formation is the process by which new species develop." This definition leads in-

evitably to the next question: "What is a species?" This question has bothered taxonomists and biologists alike ever since biologists, especially Linnaeus, firmly established the species concept, but the confusion has grown steadily with the constant refinement of taxonomic technique and with the advent of evolutionary thought. Unfortunately, we can not dispose of the question simply by dodging the definition as irrelevant, because, for example, a good many controversies are primarily due to the different species concepts held by the opponents (*cf.* Goldschmidt, 1937).

The difficulties and possible objections against a species definition can best be illustrated by analyzing and criticizing a number of the definitions given by well-known taxonomists or geneticists.

To Linnaeus the species was a unit that could be defined on a morphological basis. Consequently, he described in numerous cases males and females, young and adult, as different species, because they had well-definable morphological characters. Furthermore, the species was for him, in general, the lowest systematic unit. I do not have the time to trace the historical changes of the species concept. It has been done by Stresemann (1936) so far as ornithology is concerned. There is no doubt, however, that the species concept in most taxonomic groups has undergone an almost revolutionary change during the last thirty to forty years. Painstaking taxonomic work, particularly by ornithologists, lepidopterologists and conchologists, has shown that gliding intergradation connects most geographically representative species, so that they had to be reduced to subspecies. In Darwin's day the discovery of such transitions was hailed as proof of the change of one species into another. Nowadays we know that it is the normal condition and that there are relatively few "good" species that are not actually composed of groups of "subspecies." A few taxonomists, especially entomologists, are left who still insist in calling species the lowest

systematic categories. The best-known advocate of this is Kinsey (1937b) whose point of view is as follows:

Confusion will be avoided if we call the basic taxonomic unit the species. It is the unit beneath which there are in nature no subdivisions, which maintain themselves for any length of time or over any large area. The unit is variously known among taxonomists as the species, subspecies, variety, *Rasse* or geographic race. It is the unit directly involved in the question of the origin of species, and the entity most often indicated by non-taxonomists when they refer to species. Systematists often introduce confusion into evolutionary discussions by applying the term to some category above the basic unit.

Goldschmidt (1937) has already voiced some objections to these claims, but I might add a few remarks. It is not true that "there are in nature no subdivisions" below the species [of Kinsey], "which maintain themselves for any length of time." Actually there are all degrees of distinctness between "the effective breeding population" within a continuous array of populations and the subspecies which is completely isolated by geographical barriers. Recent genetic work (Dobzhansky, *et. al.*) as well as Kinsey's own taxonomic work shows this quite clearly. Furthermore, the lowest category is not "the entity most often indicated by non-taxonomists when they refer to species." When the layman or non-taxonomic biologist speaks of "the song sparrow," he is not concerned with the numerous subspecies of this species, as for example the Atlantic, the Eastern or the Mississippian race. He means the total sum of all these races, or else, the particular local race wherever he meets it. Neither do we call the human races species, although they are the basic taxonomic units of *Homo sapiens*.

Emerson's definition (1938), I am afraid, is equally vulnerable. He says: "A species is a genetically distinctive, reproductively isolated, natural population." To begin with, every "natural population," no matter what its rank is, that has yet been genetically analyzed, has turned out to be "genetically distinctive." Every individual (unless it be an identical twin) has an overwhelming chance to be genetically distinct from every other member of his own species due to the almost infi-

nite possible combinations of alleles, and therefore the genetic distinctness is of no great value in a species definition. More difficulties are provided by the clause "reproductively isolated." The chief trouble with this is that it can rarely be tested. In the tropics, for example, birds of many species are exceedingly sedentary. If two populations of one species occupy two separated mountain-tops or islands, they are unquestionably "reproductively isolated," as effectively as is conceivable. Still some major climatic change could bring them together again and they would unquestionably freely hybridize on meeting each other. Artificial breeding experiments might not solve anything in such a case, because in captivity related species are known to hybridize which fail to do so in nature. This is known for *Cepaea hortensis* and *nemoralis* which in nature commonly live side by side with hybrids being exceedingly rare, and also for many species of birds.

Timoféeff (1940) overcomes most of the difficulties of other definitions but is equally weak against the last of the objections just stated. He writes:

A species is a group of individuals that are morphologically and physiologically similar (although comprising a number of groups of the lowest taxonomic category) which has reached an almost complete biological isolation from similar neighbouring groups of individuals inhabiting the same or adjacent territories. Under biological isolation we understand the impossibility or nonoccurrence of normal hybridisation under natural conditions.

Most geographically isolated forms would be species under this definition. Dobzhansky (1937) wants to overcome this difficulty (which he realizes very clearly) when he defines species as: "that stage of the evolutionary process at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding." This definition is an excellent description of the process of speciation, but it defines what a group of species is (*i.e.*, two or more separate arrays), not what *one* species is. I do not share Emerson's (*l.c.*) objections (production of fertile offspring between re-

lated species), because a modern ornithologist does not consider as full species two neighboring "species" which hybridize freely in their zone of contact. My principal objection against Dobzhansky's definition is that he leaves difficult situations of practical importance undecided. For example, how does his definition deal with those cases where a species (in the widest sense, not in Dobzhansky's) consist of a long geographical chain of different populations or subspecies, of which each one intergrades with its neighbors and is not separated by any physiological isolating mechanisms, but where the final members of the chain are completely sterile when brought together. There are several such cases known from beetles (*Epilachna*, *Carabus*) and a number of less drastic ones from other groups. Second, how can it be practically tested that two forms are "physiologically incapable of interbreeding"? There are probably more than a million species of animals in existence and in less than 1/10 of 1 per cent. have crosses with one another been attempted. Should we wait until the other 99 9/10 per cent. have been crossed before these species can be fully established?

Before I try to give my own species definition we might analyze very briefly what criteria are generally used to define species.

(a) *Morphological characters*: Descriptive characters, such as structure, proportions, color patterns, etc., are the conventional means used to define a species. It is therefore only natural if even modern species definitions state that a species is composed of "groups of individuals with similar morphological characters." However, geographical forms differ in certain families (*Phasianidae*, *Paradisaeidae*, *Trochilidae*) by "stronger" morphological characters than good species in others (*Apodidae*, *Tyrannidae*, *Zosteropidae*). Perfectly good species are often remarkably similar, I only need to remind you of *Drosophila pseudoobscura* and *D. miranda*, while in other cases the extreme links of a long chain of subspecies are

more different from each other than are most related species. Rensch (1929, 1938, 1939a) has pointed out that nearly every morphological character which has been used to separate species may also vary geographically within the species. Furthermore, morphological characters often vary independently from fertility and are therefore of no value in the all-important border-line cases. Morphological characters are, therefore, of no decisive value in a species definition, because *there is no difference between subspecific and specific characters*.

(b) *Genetic distinctness*: In the earlier years of the science of genetics, great stress was laid on the genetic distinctness of two species. Now we know, not only that all subspecies are genetically different, but also the populations within the subspecies (Dobzhansky for *D. pseudo-obscura*, Sumner and Dice for *Peromyscus*, Goldschmidt for *Lymantria dispar*, etc.). In fact every individual is a different biotype. We readily admit this in regard to man and domestic animals and plants, but it is equally true for all other animals. Genetic distinctness, being a *sine qua non* condition, is therefore of little value in a species definition.

(c) *Lack of hybridization*: This criterion is only of limited value. If no hybridization is possible between two neighboring populations, then there is little doubt that they are good species. The opposite condition is, however, not an absolute necessity. Many good species of animals are capable of producing hybrids in captivity, but never interbreed in nature.

A successful species definition should not lay too much stress on any one of the three above-listed criteria. Of all the definitions that have come to my attention within recent years, the one proposed by Sewall Wright (1940) seems to show the fewest flaws. According to him species are "groups within which all subdivisions interbreed sufficiently to form intergrading populations wherever they come in contact, but between which there is so little interbreeding that such populations are not found." This

definition again omits reference to those "subdivisions" which have the misfortune of not being able to come in contact with other subdivisions because they are spatially or ecologically isolated.

One might therefore propose the following emended definition: "*A species consists of a group of populations which replace each other geographically or ecologically and of which the neighboring ones intergrade or hybridize wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers.*" Such a definition is applicable in practically all difficult cases of bird taxonomy except where the terminal links of a chain of races overlap (see below). It remains to be seen how useful it is when applied in other groups, although Remane (1927), who is not an ornithologist, arrived at a very similar formulation. As a taxonomist, I am, of course, interested in a practical definition, and a definition like Dobzhansky's is of little use in taxonomic work. Even the above given formulation is at best only an approach. In many cases of interrupted distribution it is necessary to leave it to the judgment and the systematic tact of the individual taxonomist, whether or not he considers two particular forms as "potentially capable" of interbreeding, in other words, whether he considers them species or subspecies. Furthermore, the just given definition applies to "biological or zoogeographical species." The taxonomist finds it sometimes useful for practical purposes to treat as full species what should be regarded as subspecies on the basis of the definition. Groups of such "semi-species" are called superspecies in the subsequent discussions (Mayr, 1931) (see also Rensch, 1934).

THE REALITY OF SPECIES

The discussion of various species definitions, having resulted in the conclusion that it was impossible to propose a completely satisfactory definition, must have

raised some doubt as to whether there is such a thing as species. As a matter of fact the opinion is very prevalent among non-taxonomists that "species" are just idealized abstractions, created by the taxonomist for his own convenience. This point of view may apply to the situation in little-worked groups of invertebrates, but it does not apply to the more thoroughly investigated systematic groups. The construction of a comprehensive, lucid species definition may present many difficulties, but in reality the species themselves are remarkably real natural phenomena (Dobzhansky, 1937).

A. INDIVIDUAL VARIATION AND SPECIES DELIMITATION

The taxonomist, in the course of his work, is generally confronted by two classes of difficulties when he tries to define the natural limits of his species. The first is caused by the evolutionary instability of species, and will be treated subsequently, while the second is caused by individual variation. The latter kind of difficulty is usually removed, as soon as sufficient material is available. It is quite amazing that in well-worked groups there is hardly ever any doubt what is a species and what not, even though there are no absolutely reliable species criteria in existence. In disputed cases the final decision usually shows that either (1) several stages or phases of a species are so different that they had been mistaken for different species or (2) just the opposite, that several species which occur in the same locality are so similar that they were considered stages of one species.

(1) *Phase confusion*: That stages or phases of one species are so different that they have been considered for a long time to belong to several species is a frequent occurrence in marine and fresh-water animals, as well as in insects. It is, however, also a common occurrence in birds. Linnaeus described the adult (= barred) plumage of the goshawk as *A. palumbarius*, the immature (= streaked) plumage of the same species as *A. gentilis*. I could quote dozens of similar cases where young and

adults or male and female were described as different species until closer study revealed the error. More difficult are the cases where strikingly different color phases occur in the same species, such as wild type and white birds, or wild type and melanistic, etc. Stresemann (1926) summarized (with colored plates) some of the more interesting cases. The number of such cases has been more than doubled in the last fifteen years and some highly unusual alternative plumages have been described (for example, tail-coloration in *Rhipidura brachyrhyncha*, Mayr and Rand, 1937). If such color phases are restricted to definite parts of the range of the species, particularly to the exclusion of the "wild" type, the difficulty is still greater. Two well-known "pairs" of species of North American birds seem to fall into this category (only 2 out of about 755!). The great white heron (*Ardea occidentalis*) is now considered specifically distinct from the great blue heron (*Ardea herodias wardi*), and the lesser snow goose (*Chen h. hyperboreus*) from the blue goose (*Chen caerulescens*), but I am confident that in both cases it will eventually be shown that the white partner of the pair is merely a color phase (mutant) which has become more or less restricted to a definite region.

(2) *Sibling species*: The opposite condition exists where pairs or larger groups of related species are so similar that they are generally considered as one species, or at least have in the past for a long time been mistaken for one another. Several such incompletely analyzed species groups are known from the genus *Drosophila*, for example, *Drosophila* "obscura" and "affinis." The species of the flycatcher genus *Empidonax* are the closest to this situation that we find among North American birds, although this case was completely settled more than a generation ago. From Europe two pairs of exceedingly similar species of birds are known, the two chickadees (*Parus atricapillus* and *palustris*) and the two creepers (*Certhia familiaris* and *brachydactyla*). Again

the differences in morphology, ecology, habits and distribution were largely cleared up more than forty years ago. So far as birds are concerned there are no more species difficulties of this sort in the better-explored parts of the globe. In the tropics and in the southern hemisphere there are a number of genera with extraordinarily similar species. Some of these have been recently monographed and the situation has been clarified; the most notable cases are the steamer ducks (*Tachyeres*) (Murphy, 1936), the grass warblers *Cisticola* (Lynes, 1930), the flycatcher *Cyornis* (several authors), the honey-eaters *Meliphaga analoga* and allies (Rand, 1936a) and the South American *Scytalophus* (Zimmer, 1939). There are, however, still a few genera left (for example, the cave swiftlet *Collocalia* with about sixteen species) in which only two or three specialists can even approximately identify the various species. Considering that there are about 8,500 species of birds in the entire world, the number of "difficult" species does not even amount to 1 per cent. The eventual elimination of all such cases may perhaps be considered the most tangible result of taxonomic work.

B. SPECIES IN THE "MAKING"

Another class of difficulties, however, will never be eliminated. We have in birds a high number of cases, where certain populations become detached from the main body of their "parent" species, by becoming isolated on an island, on a mountain or through some other geographical or ecological barrier, and develop characters during this period of isolation which deviate considerably from those of the parent species. Such "forms" (to use a neutral term) are geographical representatives of their next relatives and show the common origin still very clearly. Usually there is considerable taxonomic disagreement about these forms, the more radical authors calling them subspecies, the more conservative ones, good species. We fail miserably if we try to apply the test of species definition to such forms.

It is of interest to find out how common such cases are. I have made an analysis of all the North American birds listed in the A. O. U. Checklist (1931), a work which is rather conservative in its taxonomic point of view. I have omitted only introduced species and the purely marine order Tubinares. In 374 genera there are 755 species with a total of 1,367 species and subspecies. At least 94 of the listed 755 full species of North American birds will be considered by some authors to be merely subspecies of other species. In other words 12.5 per cent. of the species of North American birds have reached a very interesting taxonomic stage: They still show by their distribution and general similarity that they had been only recently geographical forms of some other species, but they have, in their isolation, developed morphological characters of such a degree of difference that the majority of authors now prefers to call them good species. Typical examples in the North American bird fauna are: Ipswich and Savannah sparrow (*Passerculus*), red-shafted and yellow-shafted flicker (*Colaptes*), Audubon's and myrtle warbler (*Dendroica*), the various species of the genera *Junco* and *Leucosticte*, etc. The majority of these forms are more or less isolated, either on the islands off the California coast or on the various mountain ranges of the Rocky Mountains or in the lowlands east and west of the Rocky Mountains. These "semi-species" comprise $12\frac{1}{2}$ per cent. of the total of species in the rather continental fauna of North America. For a typically insular region, namely the Lesser Sunda Islands, Rensch (1938: 275) thinks that not less than 47 species are intermediate among a total of 160 species. I have analyzed the birds of the Solomon Islands and find that if we employ a narrow species concept there are 174 species of land and fresh-water birds; if we, however, employ a wide species concept (= include within one species all geographical representatives) there are only 125 species. In other words, of 174 species there are 49 of intermediate status, that is 28.2 per cent.

I have used birds to illustrate this situation, because the highly refined condition of bird taxonomy permits the quotation of exact figures. The phenomenon as such is, of course, equally present in many other taxonomic groups. Goldschmidt (1937), for example, has called attention to the fact that many of Kinsey's "higher categories" of Cynipidae are nothing more than strongly evolved geographically representative forms. It is only "a matter of taste" whether we designate such isolated and distinct forms subspecies or species. No species definition has yet been found—and I am quite certain that none will ever be found—which will satisfactorily cover such cases.

But let us now examine under what conditions these border-line cases may have developed. Let us follow the entire course of the speciation process, as revealed by the sequence of the lower systematic categories. To do this we must pay particular attention to geographical variation.

GEOGRAPHICAL SPECIATION

Geographical variation is now generally considered to be one of the most important phenomena of evolution. The refinement of modern taxonomic research as well as the stimulus given by the development of genetics have had the result that population studies are very much in vogue, or as the taxonomist puts it "the comparison of series from various localities." This type of study usually leads to the conclusion that no two populations of a species are quite alike. Of the variation of a species of *Peromyscus*, Dice (1939) recently said:

The mice of no two localities are quite alike either in average body dimensions or in average . . . pelage color. Local variability of a similar kind occurs in all the species and races of *Peromyscus* which have been critically studied.

Such a statement would be valid in principle for nearly every species of mammal or bird and probably for all species of organisms. These were laboratory-bred animals reared under standard conditions and there is no

doubt that the variations among the local populations were of a genetic nature. These differences of the means, however, are merely of statistical value, and are not sufficient to enable us to identify individuals. Consequently, such populations will be united under one subspecific name.

We sometimes unite even fairly distinct forms if the variants are distributed in a highly irregular manner. Any taxonomic character, such as pigmentation, patterns, proportions, etc., may show such irregular distribution, but it is most easily demonstrated if cases of simple size variation are selected. The accompanying map (Fig. 1)

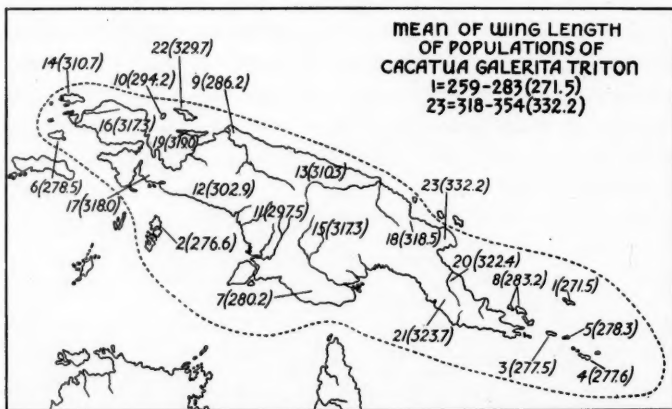


FIG. 1. Irregular variation within the range of one subspecies. The smallest and the largest of 23 populations are very different, but the gap is bridged by intermediate populations.

of 23 populations of the cockatoo *Cacatua galerita triton* (Mayr, 1937) and the table of 10 populations of the

IRREGULAR SIZE VARIATION OF THE HONEYEATER *Foucheaio carunculata* IN CENTRAL POLYNESIA

	Males	Females
Ono ilau (E. Fiji) ¹	108-113 (110.0) ²	96, 97 (96.5)
Tonga Islands	104-114 (108.3)	92-101 (95.6)
Southern Lau Archipelago (E. Fiji)	103-110 (106.9)	89- 98 (93.9)
Tutuila (Samoa)	102-109 (105.8)	91- 97 (94.4)
Manua (Samoa)	99-107 (104.7)	92- 98 (93.8)
Matuku (E. Fiji) ¹	104, 105 (104.5)	87- 92 (89.3)
Upolu (Samoa) ¹	99-102 (100.8)	90, 93 (91.5)
Northern Lau Archipelago (E. Fiji)	99-103 (100.9)	84- 91 (87.8)
Savali (Samoa)	93-102 (98.5)	85- 92 (87.2)
Fotuna Island	93- 98 (95.9)	82- 87 (84.2)

¹ The measured series is too small to show the full range of size-variation.

² The figures indicate the length of the wing in millimeters.

honeyeater *Foulehaio c. carunculata* (Mayr, 1932) show that neighboring populations may be very dissimilar, while some very distant ones are practically indistinguishable. Sometimes in a chain of subspecies of one species, the alternate members are more similar to one another than the neighboring ones. The alternating races with cock or henfeathered females of the New Guinea wren-warbler *Malurus alboscapulatus* (Mayr and Rand, 1935) are a good illustration of this phenomenon.

Variation within continuous ranges: It does not concern us in this connection what the causes are of the genetic differences between populations. Chance losses of genes or alleles and fixation of new mutations partly in connection with selective forces of various sorts, are the factors that are usually quoted, although the belief in some kind of direct influence of the environment is still held by some taxonomists and will continue to be held in the future, until somebody finds convincing proof against it.

If we compare a series of neighboring populations or subspecies of one species, we often find that the differences between them are arranged in a graded series, for example, the easternmost form are palest, the westernmost darkest and all the in-between populations form a connecting series. J. Huxley has recently introduced the term *cline* for such a character gradient, but the phenomenon as such has been known and studied for more than a hundred years. The character gradient runs in most cases closely parallel to some climatic gradient and can be interpreted as being due to adaptive responses to selective factors in the environment. I shall not go into details since we have several admirable recent summaries (Rensch, 1936, 1939b; Huxley, 1939).

This interpretation can not, however, be applied when there is no evidence for an environmental gradient as, for example, in the case of some tropical clines known to me: *Rhagologus leucostigma*, *Paradisaea apoda* (see Fig. 2), *Gallicolumba* in Micronesia-E. Polynesia, etc. So far no

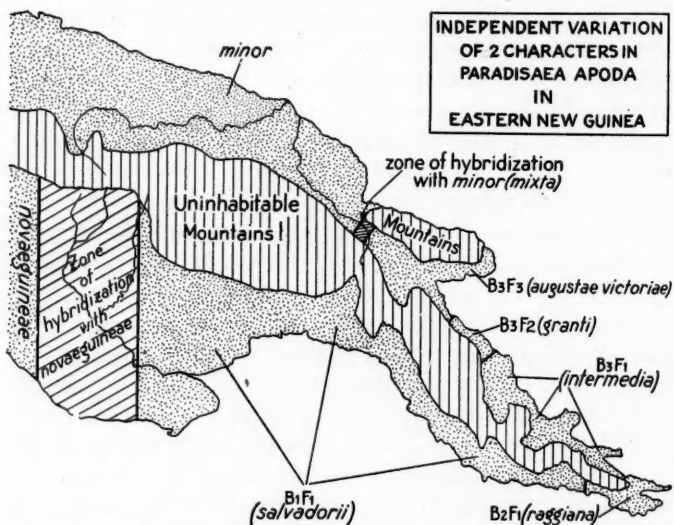


FIG. 2. A cline that is independent of environmental gradients. B. = Coloration of Back, B1, entire back brown, B2, upper back yellow, lower back brown, B3, entire back yellow. F. = Coloration of the plumes (flank feathers), F1, red, F2, orange-red, F3, orange.

successful interpretation is known to me, but instability of certain genes and gene loss in the border populations of an expanding species will have to be included in forming an interpretation.

We speak of irregular geographical variation wherever such character gradients (clines) are not discernible. Since most character gradients are correlated with climatic gradients, it is only natural that clines should be absent or little pronounced where species ranges are recent (selection has had no time yet to work) or where there are no environmental gradients, such as in wide parts of the humid tropics. Irregular variation, as is often found on tropical archipelagos, is very inconvenient to the taxonomist, as I have already pointed out in the cases of *Cacatua* and *Foulehaio*.

The phenomenon that an animal is evenly distributed throughout its range is an ideal that is practically never realized. Even the most wide-spread and common spe-

cies show gaps in their ranges and modern population studies have shown that the actual distribution picture resembles more that of clusters of little colonies than anything else. Even so there is usually so much interchanging of individuals between the neighboring and insufficiently isolated populations that the range is continuous for all practical purposes. In species with such continuous ranges we usually encounter the following phenomena (Goldschmidt, 1935; Kinsey, 1937a): (1) No clear-cut subspecies are formed. (2) Individual variation is high. (3) Each population is more or less intermediate between its neighbors. (4) There tends to be a gliding change of characters (clines), with an infrequent insertion of noticeable steps. (5) Some characters are curiously independent from the general trend within this range and show irregular variation. These points are of interest to the taxonomist, but they will also have to be considered by the geneticist. Species formation proceeds very slowly wherever such continuous ranges are involved and rarely goes very far.

The effect of discontinuous distribution: Up to now we have been dealing with fairly continuous ranges of populations, but *isolation* is required in addition to variation before significantly different forms can develop. This is not the place to discuss all the various isolating mechanisms that are found among birds; I shall restrict myself entirely to a discussion of the effects of *geographical isolation*. There is no case known in birds where geographical isolation was *not* the primary isolating mechanism. All the other isolating factors, such as ecological, psychological, cytological and genetic ones, can develop in birds only when a form is isolated and withdrawn from the interchange of individuals between neighboring populations. Such an isolation can occur either on true islands or other insular locations, such as on mountain ranges or in grassland islands within the tropical rain forest or in patches of forest within savannas, etc. (Birds are potentially good fliers and it might seem peculiar that

they should "stay put" on these distributional islands. I have quoted in a recent paper (Mayr, 1933) a number of cases of the effectiveness of natural barriers and the consequent isolation. A more detailed discussion is given by Stresemann (1927-1934, p. 635). A distribution map of a group of closely related species of *Zosterops* will illustrate this point better than any words could do (Fig. 3). Another excellent illustration of this phe-

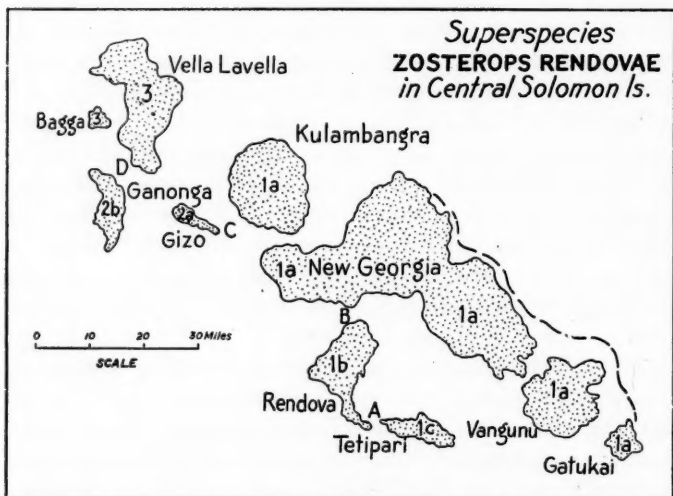


FIG. 3. Extreme localization of related species and subspecies in a tropical archipelago. 1 = *Zosterops rendovae* + subsp., 2 = *Z. z. luteirostris* + subsp., 3 = *Z. z. vellavellae*. A = 1.7 km., B = 2 km., C = 6 km., and D = 5 km.

nomenon is the map of the distribution of the closely related species of the flycatcher *Pomarea* in the Marquesas Islands (Murphy, 1939).

The effect of such isolation is invariably speciation in all its stages. Some of the factors which determine the degree of differentiation are the following, four of them external and one internal.

External

- (1) Age of the island,¹ that is, the time interval since settlement by the particular species.
- (2) Size of the island, that is, size of the effective breeding population.

¹ Island in this connection means distributional, not geographic island.

- (3) Amount of competition, predation and other retarding selective factors.
 (4) Effectiveness of isolation, that is, amount of pollution by subsequent immigrants of the same species (swamping).

Internal

- (5) Inherent stability *vs.* mutability of the species.

Unfortunately, no studies are available, in which all these factors have been analyzed for a single island nor in a comparative manner for a group of islands. A forthcoming paper by D. Lack (1940) sheds some light on the relative importance of these factors among the finches of the Galápagos Islands. I myself (with de Schauensee, 1939) have shown in purely descriptive manner that speciation is a continuous process. Speciation on the two oceanic islands of Biak (near New Guinea) and Rennell (near Solomon Islands) is illustrated by the following table (including only the resident land and fresh-water birds).

STAGES OF SPECIATION ON TWO OCEANIC ISLANDS

	Biak Isl. All birds	Rennell Isl. All birds	Rennell Isl. Passeres only
No differentiation	20 = 29%	7 = 21%	1 = 8.5 %
Slight differentiation	11 = 16%	7 = 21%	0 = 0%
Endemic subspecies	29 = 43%	15 = 44%	7 = 58 %
Endemic species	8 = 13%	4 = 12%	3 = 25 %
Endemic genera	0 = 0%	1 = 3%	1 = 8.5 %
Total species	68 = 100%	34 = 100%	12 = 100%
Distance from mainland	60 km.	145 km.	145 km.

Similar tabulations could be made for mountain birds. The warm lowlands are effective barriers for animals which are adapted to the particular climatic and ecological conditions only found in the mountains.

If we take three rather isolated mountain ranges in New Guinea, the Arfak, Cyclop and Saruwaged Mountains, all three comparatively well explored, and analyze the passerine birds we find the following figures:

DEGREE OF ENDEMISM ON THREE NEW GUINEA MOUNTAINS

Mountain species Passeres	Arfak	Cyclop	Saruwaged
Not endemic	36 = 40.4%	21 = 72.4%	59 = 68.6%
Endemic subspecies	46 = 51.8%	8 = 27.6%	23 = 26.7%
Endemic semi-species ¹	6 = 6.6%	0 = 0 %	3 = 3.5 %
Endemic full species	2 = 2.8%	0 = 0 %	1 = 1.2%
Total species	89 = 100 %	29 = 100 %	86 = 100 %

¹ Under semi-species, I understand, in this connection, a species which replaces geographically some other species, but is morphologically too different to be called a subspecies.

But even most of those species which are listed as "not endemic" are slightly different on each mountain range, only the differences are below the "taxonomic threshold."

BORDERLINE CASES

Well-isolated subspecies often diverge to such a degree that they are either on the borderline between subspecies and species or else that they are considered good species even by the progressive taxonomist although they still reveal their origin as subspecies. Four different classes of such borderline cases are in this connection of particular interest to us.

(a) *Ecological representation*: This phenomenon is common in insects and other lower animals, but rare in vertebrates. The ecological representation of two subspecies of *Peromyscus* is often quoted, but there is, so far as I know, nothing exactly comparable in birds. The closest approach is perhaps that of *Melospiza melodia* (song sparrow) of California where along San Francisco Bay one subspecies is restricted to the salt marsh and another one, which is very distinct, to the dry hillsides. In this case the ecologically representative forms are still subspecies. In another case the ecological representatives are now species and even though morphologically very similar, have different voices and other habits: The king rail (*R. elegans*) of the eastern United States inhabits fresh-water marshes and the clapper rail (*R. longirostris*), salt marshes. Many cases from the Palearctic Region have been recorded by Dementiev (1938).

Similar conditions seem to prevail in South Australia, where the wooded Mt. Lofty Range with its endemic races is like an island in the savanna with its races of the same species (*Sericornis frontalis*, *Acanthiza pusilla*). Actually, this case is not strictly ecological but also altitudinal representation. That birds of higher altitudes in the same mountain range belong to a different subspecies than the birds of the same species at a lower altitude is

not uncommon, particularly in certain parts of the tropics where birds are highly sedentary on account of ill-defined seasons. There is usually a gradual change from the lowland to the high-altitude population, but occasionally there are definite breaks, such as have been described from eastern New Guinea between *Philoprora guisei guisei* and *perstriata*, and between *Melidectes belfordi belfordi* and *brassi* (Rand, 1936b). Both *perstriata* and *belfordi* are well-defined races which are restricted to the mountain tops above 3,000 m, and whose range is now broken up into a number of islands, separated at a lower altitude by the continuous range of *guisei* and *brassi*. Similar cases have been described from the border of Tibet and Szetchuan, where the fauna of the Hsifan Mountain Forest and the Tibetan Plateau meet. *Phylloscopus fuscatus fuscatus* and *weigoldi* and *Ph. affinis* and *subaffinis* (Ticehurst, 1938: 89) are examples from this region. It is very probable that the ecological isolation was preceded in all these cases by geographical isolation. Theoretically in the same class are many of the highland races of the Roraima-Duida Plateaus of South America, which although often only separated by a cliff of 3,000 feet, are as different from their low altitude representatives as good species and are treated as such by the more conservative taxonomists (Chapman, 1931).

(b) *Extreme morphological development*: Populations of the same immediate common origin, but replacing each other geographically are, if different, generally called subspecies by the modern taxonomist. The old-fashioned criterion of intergradation by actual contact or (in cases of isolation) by individual variation is no longer demanded. But there are some cases where even the most inveterate "lumper" stops. They are the cases where certain subspecies, during periods of long and efficient isolation, have developed such a degree of difference that they might be considered different genera if only morphological criteria were used. As a matter of fact, a great many isolated forms have originally been described as

different genera and it is only recently that their true systematic position has become clear. I am illustrating it with the case of the barking pigeon (*Ducula pacifica*) of Polynesia, which has developed a form (*galeatus*) on the Marquesas Islands, which on account of its peculiarly developed bill was, until eight years ago, considered a good genus (*Serresius*) (Fig. 4). Other genera that are

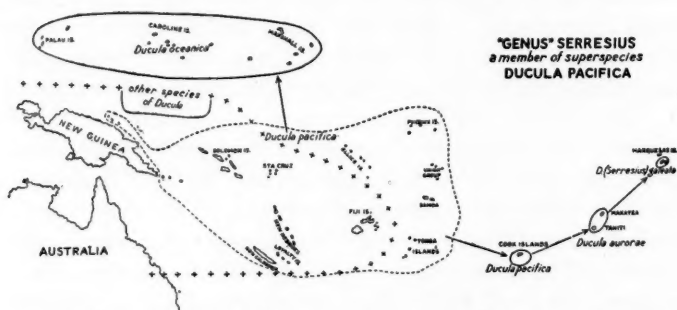


FIG. 4. Extreme differentiation of the most isolated form in the *Ducula pacifica* group.

based on morphologically distinct geographical forms are: in pigeons—*Oedirhinus* (of *Phalinopus iozonus*). *Chrysophaps* (of *Chrysoena luteovivens*); in kingfishers—*Todirhamphus* (of *Halcyon chloris*); in birds of paradise—*Astrarchia* (of *Astrapia nigra*), *Schlegelia* (of *Diphyllodes magnificus*), *Uranornis* (of *Paradisaea apoda*); in drongos—*Dicranostephes* (of *Dicrurus bracteatus*); in rails—*Porphyriornis* (of *Gallinula chloropus*); in Passeres—*Galactodes* (of *Erythropgyia*), *Conopoderas* (of *Acrocephalus*), *Pinarolestes* (of *Clytorhynchus*), *Papuoorthonyx* (of *Orthonyx*), *Allocotops* (of *Melanocichla lugubris*), etc.

In most of these cases, and they are just a small selection from the numerous cases known to me, subspeciation, that is geographical variation, has actually led to the evolution of unquestionably new species. Some of Kinsey's species of Cynipidae apparently belong to the same class. The most strongly divergent forms, that is the most specialized or most recent ones, develop invari-

ably somewhere near the border of the range. Current evolution, therefore, proves conclusively that the hypothesis of some paleontologists is wrong, that evolution is most rapid in the center of the range and that the primitive forms are pushed out toward the periphery of the range. Such may occur in a few isolated cases, but it is certainly not the rule in contemporary evolution.

(c) *Double invasions*: Oceanic islands generally derive their fauna from other nearby islands or from neighboring continents. The immigrants soon start to diverge from the original parent population (a process which is speeded up by the small size of most of these island populations) and if after a sufficient time interval, a second set of immigrants arrives from the home country, the two waves of immigrants will behave like good species. Such cases are known from nearly every group of islands, for example, Tasmania (*Acanthiza pusilla* and *ewingi*), Tenerife (*Fringilla teydea* and *Fringilla coelebs canariensis*), western Canary Isls. (*Columba laurivora* and *bollii*), Masatierra (*Eustephanus fernandensis* and *galeritus*), Norfolk Isl. (*Zosterops albogularis*, *Z. tenuirostris*, *Z. lateralis norfolkensis*), Marquesas Isls. (*Ptilinopus mercieri* and *dupetithouarsi*) (Fig. 5), Samoa (*Lalage maculosa* and *sharpei*), Onga

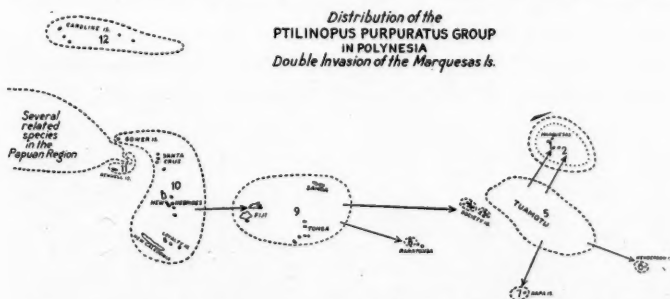


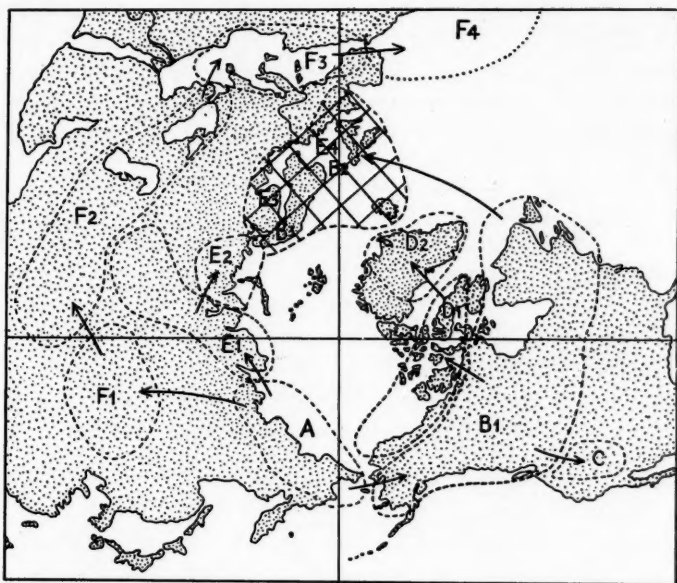
FIG. 5. Illustration of a case of double invasion in the genus *Ptilinopus*. 1 = *dupetithouarsi* + subsp., 2 = *mercieri* + subsp., 3 = *purpuratus*, 4 = *chrysogaster*, 5 = *coralensis* + subsp., 6 = *insularis*, 7 = *huttoni*, 8 = *rarotongensis*, 9 = *porphyraceus* + subsp., 10 = *greyi*, 11 = *richardsii* + subsp., 12 = *ponapensis* + subsp.

Levu, Fiji (*Mayrornis versicolor* and *M. lessoni orientalis*) (see also Stresemann, 1927-1934, p. 646, and

Mayr, 1933). Not a single case is known to me from recent islands, such as England or Ireland. On the other hand, the fauna of ancient archipelagos, like Hawaii and Galápagos, is composed of whole clusters of such species. In many cases they are still so similar to one another that they would probably be considered subspecies if they occurred on neighboring islands instead of on the same island.

The just quoted cases are the successful ones. Subsequent invasions originating from the parental stock are probably much more frequent than these few cases indicate, but the new settlers are quickly absorbed by the daughter population, because the latter had not yet developed into a new species. If entire subspecies meet on intermediate islands, complete hybrid populations result, such as I have described for *Megapodius* (Mayr, 1938) and in two cases for the genus *Pachycephala*.

(d) *Overlap*: The perfect demonstration of speciation occurs, of course, when a chain of intergrading subspecies forms a loop or an overlapping circle, in which the forms which co-exist in the same locality no longer interbreed. There is no better way than this to demonstrate the effectiveness of geographical variation. Unfortunately, there are not many complete cases. The best one in birds is probably that of *Parus major* (Rensch, 1933). Another good case is that of the herring gull group (*Larus argentatus*) (Stegmann, 1934). The races of this species are arranged in a circumpolar ring, but *Larus argentatus*, coming from America, invaded western Europe and lives now side by side with *Larus fuscus*, like a good species, although the two "species" are connected by a chain of intermediate forms in Siberia and North America (Fig. 6). Not quite so clear is the case of *Halcyon* in Micronesia (Fig. 7). Another interesting case, relating to two species of *Zosterops* in the Lesser Sunday Islands, was described by Stresemann (1939). The two honey buzzards of the Philippines (*Pernis celebensis steerii* and *Pternis ptil. philippensis*) are also con-



OVERLAP OF THE TERMINAL LINKS OF A CHAIN OF RACES OF *LARUS ARGENTATUS*

FIG. 6. Circumpolar projection of the ranges of forms of the *Larus argentatus*-group. A = *vegae*, B1 = *smithsonianus*, B2 = *argentatus*, B3 = *omissus*, C = *californicus*, D1 = *thayeri*, D2 = *leucopterus*, E1 = *heuglini*, E2 = *antellus*, E3 = *fuscus*, E4 = *graellsii*, F1 = *mongolicus*, F2 = *cachinnans*, F3 = *michahellis*, F4 = *atlantis*. *L. fuscus* (+ *graellsii*) lives now like a good species besides *L. argentatus* (+ *omissus*).

nected in Malaysia by a ring-like chain of intermediate forms.

THE STAGES OF GEOGRAPHICAL SPECIATION

The point which I have tried to illustrate in the preceding discussion is that there is every condition existing between an almost uniform species and one in which isolated populations have diverged to such a degree that they can just as well be considered as separate good species. The tabulations of the level of speciation reached by various species on isolated oceanic islands (p. 267) and in mountain ranges (p. 267) show clearly that geographical speciation is by necessity linked up with and influenced by geographical factors. In consequence, the

actual process that leads to the development of new species, the time required for it, etc., is somewhat different not only in every species, but also in every geographical district. A worker who confines his studies to one particular region may not and will not get a complete picture

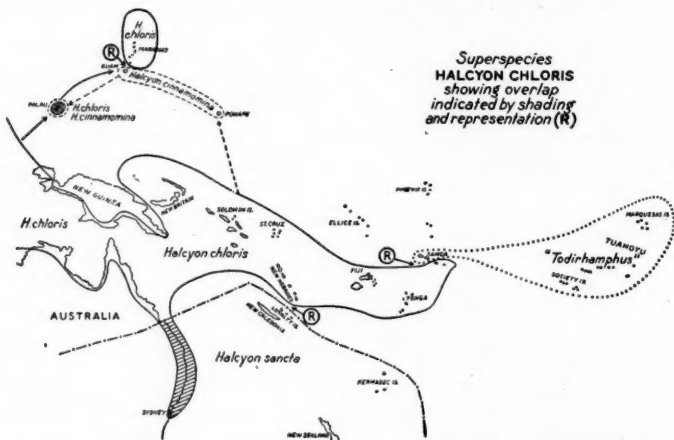


FIG. 7. The closely related kingfishers of the superspecies *Halcyon chloris* still replace each other geographically (R), except on two places: Palau Island and the coast of eastern Australia. In both locations two forms live side by side like good species.

of these phenomena. I have been thinking how I could best demonstrate this point and have arrived at this solution.

It is possible to generalize and simplify the diversified phenomena of evolution and to classify all species of birds according to the degree of speciation which they have reached. Such a classification is based on a simplified outline of the process of evolution, for example, as follows:

Stage 1: A uniform species with a small range
followed by

Process 1: Expansion of range
resulting in

Stage 2: A uniform species with a large range
followed by

Process 2: Differentiation into subspecies
resulting in

Stage 3: A geographically variable species with a more or less continuous array of similar subspecies (3a all subspecies are slight, 3b some are pronounced)

followed by

Process 3a and 3b: Development of geographical barriers between some of the populations; also: Development of isolating mechanisms in the isolated and differentiating subspecies

resulting in

Stage 4: A geographically variable species with many subspecies completely isolated, particularly near the borders of the range, and some of them morphologically as different as good species

followed by

Process 4: Expansion of range of such isolated populations into the territory of hitherto strictly representative forms

resulting in

Stage 5: Overlapping ranges of closely related species either of which might be in any of the stages 1-4.

The taxonomist will be principally interested in stages 1-5, the ecologist and zoogeographer in processes 1, 3a and 4 and the geneticist in processes 2 and 3b. Species in nature are, of course, not always clearly referable to one or the other class, as I have defined them above. Not only are some of them between two stages but also very often one half of the range of a species is in one stage, the other half in another stage. There are also those cases of ring-like chains of forms which are difficult to fit into the above given classification.

It is possible, in spite of all these difficulties and objections, to take the entire number of species of a systematic group (let us say birds or butterflies) from one particular region and divide them up according to the stage of speciation to which they belong. (Stage 5 will have to be treated separately, because overlapping species will be considered as full species and be listed in classes 1-4.) The resulting figures of such an analysis shed much light on the degree of speciation in the respective regions. To demonstrate the value of this method, which is only applicable to thoroughly well-known groups, I am tabulating the passerine birds of three geographical regions, including the extra-territorial range of each species. For

practical reasons I have subdivided species with weak (3a) and with pronounced (3b) subspeciation.

DEGREES OF SPECIATION IN DIFFERENT GEOGRAPHICAL REGIONS

Stage	Manchuria ¹ (continuous ranges)	New Guinea region (partly continuous ranges)	Solomon Islands (discontinuous ranges)
	No. of species	No. of species	No. of species
1	2 = 1.9%	34 = 11.7%	9 = 18%
2	15 = 14.0%	21 = 7.2%	1 = 2%
3a	59 = 55.1%	118 = 40.7%	11 = 22%
3b	30 = 28.0%	84 = 29.0%	12 = 24%
4	1 = 1.0% ²	33 = 11.4%	17 = 34%
Total	107 = 100 %	290 = 100 %	50 = 100%

¹ Including all relatives within the Holarctic Region.

² Actually this is a case of discontinuous distribution, because it relates to a representative species on the Bonin Islands.

An analysis of this tabulation shows that stages 4 and 1 which indicate the final stages of evolution, are practically non-existent where geography and geology favor continuous ranges. On the other hand, stages 2 and 3a, indicating the early stages of evolution, reach a definite high in such continental areas. In contradistinction we find that where geographical factors break up the species ranges to a high degree, as, for example, on an old tropical archipelago such as the Solomon Islands, a great number of the species are in the final stages of evolution (4 and 1) and comparatively few in the early stages (2 and 3a). A student of speciation must study both regions with continuous and discontinuous ranges before he can generalize on the dynamics of the speciation process. To base all conclusions on the Palearctic or the Nearctic regions leads inevitably into error, because these two regions show special conditions: There are few effective geographical barriers and many of the present ranges were comparatively recently occupied, that is after the retreat of the ice. All the workers who believe that geographical variation does not lead to species formation, base this opinion on research done in the Holarctic Region. However, I believe that I have quoted sufficient examples to show that geographical variation does lead to formation of new species, provided that it is coupled with isolation.

LITERATURE CITED

A. O. U. Check-List

1931. "Check-List of North American Birds." Fourth edition.

Chapman, F. M.

1931. *Bull. Amer. Mus. Nat. Hist.*, 63: 28-58.

Dementiev, G. P.

1938. *Proc. Eighth Intern. Ornith. Congr. Oxford*, pp. 243-259.

Dice, L. R.

1939. *Contr. Lab. Vert. Genetics*, No. 9: 12.

Dobzhansky, Th.

1937. "Genetics and the Origin of Species," p. 312.

Emerson, A.

1938. *Ecology*, 19: 153.

Goldschmidt, R.

1933. *Science*, 78: 539-547.

1935. *Naturwiss.*, 23: 169-176.

1937. *AM. NAT.*, 71: 508-514.

Huxley, J. S.

1939. *Bijdr. Dierk.*, 27: 491-520.

Kinsey, A. C.

- 1937a. *Proc. Nat. Acad. Sci.*, 23: 5-11.

- 1937b. *AM. NAT.*, 71: 206-222.

Lack, D.

1940. *Proc. California Acad. Sci.* (In press.)

Lynes, H.

1930. "Ibis, *Cisticola* Suppl.," 673 pp., 20 pl.

Mayr, E.

1931. *Amer. Mus. Novit.*, No. 469: 2-3.

1932. *Amer. Mus. Novit.*, No. 516: 4-9.

1933. *Mitt. Zool. Mus. Berlin*, 19: 320-323.

1935. *Proc. Linn. Soc. N. Y.*, 45/46: 19-23.

1937. *Amer. Mus. Novit.*, No. 947: 6-8.

1938. *Amer. Mus. Novit.*, No. 1006: 10-11.

Mayr, E., and A. L. Rand

1935. *Amer. Mus. Novit.*, No. 814: 9-11.

1937. *Bull. Amer. Mus. Nat. Hist.*, 73: 164-168.

Mayr, E., and R. M. de Schauensee

1939. *Proc. Acad. Nat. Sci. Philadelphia*, 91: 7-9.

Murphy, R. C.

1936. "Oceanic Birds of South America," pp. 951-972.

1939. *Science*, 88: 533-539.

Rand, A. L.

- 1936a. *Amer. Mus. Novit.*, No. 872: 1-23.

- 1936b. *Amer. Mus. Novit.*, No. 890: 1-14.

Remane, A.

1927. *Verh. Ges. Phys. Anthropol.*, pp. 2-33.

Rensch, B.

1929. "Das Prinzip geograph. Rassenkreise und das Problem der Artbildung," 206 pp.

1933. *Zool. Anz., Suppl.* 6: 19-83.
1934. "Kurze Anweisung zool.-syst. Studien." Leipzig, 116 pp.
1936. *Arch. Naturg.*, N. F. 5: 317-363.
1938. *Proc. Linn. Soc. London*, 150th Sess., pp. 275-285.
1939a. *Biol. Reviews*, 14: 180-222.
1939b. *Arch. Naturg.*, N. F. 8: 89-129.
- Stegmann, B.
1934. *Jour. Ornith.*, 82: 340-380.
- Stresemann, E.
1926. *Jour. Ornith.*, 74: 377-385, 5 col. pl.
1927-1934. *Aves*, "Kükenthal Handb. Zool.," VII, 2.
1936. *Auk*, 53: 150-158.
1939. *Jour. Ornith.*, 87: 161-163.
- Ticehurst, Cl. B.
1938. "A Systematic Review of the Genus *Phylloscopus*." London.
- Timofeeff-Ressovsky, N. W.
1940. In Huxley, "The New Systematics." (In press.)
- Wright, Sewall
1940. In Huxley, "The New Systematics." (In press.)
- Zimmer, J. T.
1939. *Amer. Mus. Novit.*, No. 1044: 1-18.

These symposia will be concluded with contributions by Dr. Lee R. Dice, Professor Warren P. Spencer and Professor Th. Dobzhansky in the July-August issue.

SHORTER ARTICLES AND DISCUSSION

A STATISTICAL STUDY OF TWO VARIABLES IN THE SEQUOIAS—POLLEN GRAIN SIZE AND COTYLEDON NUMBER

MORPHOLOGICAL characters commonly utilized by the taxonomist have often of necessity dealt with maxima and minima in size range or numerical range. These are very useful in indicating the spread of variations, and when they do not overlap similar characters in other species or genera, the general results are adequate. If there is a slight overlap between two related forms a more statistical treatment of the data is indicated.

It is the purpose here to show that the two variables found in pollen grain size and in cotyledon numbers, in which the extremes overlap slightly, are of the greatest significance when analyzed by statistical methods. By such treatment the mean values of random samples within sufficiently wide range are consistent, and extreme differences, when present within related genera, become at once apparent. The analyses need involve only the more simple biometric methods which are in common use (Davenport and Ekas, 1936). Means, standard deviations, standard errors, etc., are easily obtained after the routine counts are made. If the amount of material is limited there is naturally greater opportunity for discrepancies in results, but standard errors prove valuable in such cases. Just what constitutes a random sample is answered at least in part by the results of this type of treatment. The justification for letting the constants of such a sample represent the whole rests, of course, on the laws of probability.

On the basis of external morphology, the pollen of the Giant-sequoia or Big Tree *Sequoiadendron giganteum* (Lindl.) Buchholz (1939) and the Redwood, *Sequoia sempervirens* (Lamb.) Endl., is similar. Wodehouse (1935) reports the pollen to be indistinguishable in the two genera. The germinal papillae appear alike, and both have pollen with typically thin exines and thick intines. The intine swells considerably, even to the extent of bursting and thus shedding the exine if placed in water, and also in glycerin jelly if not carefully treated. Wodehouse's (1933) methyl-green-glycerine-jelly method was used in order to obtain fully expanded grains. The methyl-green stains the exine but not the intine, thus providing good contrast.

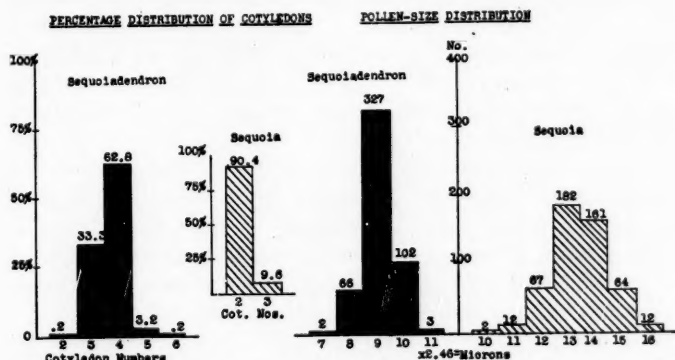
Examination of the pollen of these two genera, disclosed marked differences in size. From measurements of 500 expanded grains of each genus there appears a slight overlapping of the maximum size of pollen of *Sequoiadendron* with the minimum size of pollen of *Sequoia*. However, the mean size of the former is $22.47 \pm .05$ microns, whereas that of the latter is $32.85 \pm .11$ microns. The difference in the two means is 85 times the standard error of the difference and is of significance. Standard deviations in these counts likewise show differences, *Sequoiadendron* being $1.47 \pm .05$ microns and *Sequoia* $2.60 \pm .08$ microns. Here again the difference is significant, since a difference of more than twice the standard error is obtained, in this instance 12 times the standard error of the difference. These differences are not due to the random sampling method employed, but may be regarded as size distinctions between these two genera, possibly contingent upon the fact that *Sequoia* is a polyploid (J. T. Buchholz, 1939) whose pollen diameter may be expected to be larger than that of *Sequoiadendron*.

Using the mean diameters of both genera the volume of the *Sequoia* pollen grain is calculated to be over four times that of *Sequoiadendron*. This, however, is an approximation, since the grains are not perfect spheres, but the data tend to show a relationship similar to that found in the *Daturas* (Blakeslee, Belling and Farnham, 1923).

The two graphs showing pollen distribution are based on total counts of 500 grains in each genus. From these graphs one obtains at a glance the spread or range in sizes, the overlapping at the extremes, and can approximate the average size of the grains. The spaces on the abscissa if multiplied by 2.5 will give the diameter of the pollen grains in each category. At about 25 microns there is an overlapping in size of grains of the two genera. Most of the pollen counted of the Big Tree is found to be 22 microns in diameter. This agrees rather closely with the mean obtained ($22.47 \pm .05$). In the Redwood the greatest number of grains measure 32 microns. The mean in this instance is $32.85 \pm .11$ microns. This figure is slightly larger, but is due no doubt to the large number of grains falling within the 34.5 micron group to the right of the 32 micron group.

Number of cotyledons when reported in the literature may sometimes list minimum to maximum ranges but mean values are usually neglected. In Gordon's "Pinetum" (Gordon, 1880) the range for the Big Tree is given as 3-6 (mostly 4's) and the Red-

wood is given as 2's mostly, sometimes 3 cotyledons; Hickel (1911) in his extensive report on seeds and seedlings of conifers lists the Big Tree as having ordinarily 4 (rarely 3 or 5) cotyledons, and the Redwood is given as 2, exceptionally 3; Pilger (1926) indicates (erroneously) a range of 4-6 for both of the sequoias; but from none of these has the reader any idea how many or how few specimens were actually examined.



Graphs showing distribution of cotyledon numbers and pollen grains in the two sequoias.

A statistical study similar to that for pollen was made of the number of cotyledons of embryos of the two genera. Of 366 embryos counted *Sequoiadendron* shows an extreme range of 2-6 cotyledons with a mean value of $3.69 \pm .03$ cotyledons, whereas *Sequoia* on the basis of 248 embryos has a mean of $2.09 \pm .02$. Although the cotyledon numbers of the two genera overlap at the extremes, the difference shown is 50 times the standard error of the difference and is significant. Standard deviations also show differences, being $.52 \pm .02$ in *Sequoiadendron* and decidedly less in *Sequoia* ($.29 \pm .01$). The standard error in this case is 10 times the standard error of the difference.

Two *Sequoia sempervirens* embryos showed partial fusion of these organs, simulating a condition of cotyledonary tube formation. Another abnormality noted in this genus was found in one embryo which had a fourth cotyledon as a small protuberance arising from the region of the plumule but slightly displaced into the cotyledonary node and which was much smaller than the three average-sized cotyledons.

The graphs show the distribution of cotyledon numbers on a percentage basis, since the total number of embryos counted in each case is not the same. The Big Tree (*Sequoiadendron*) shows a range from 2-6 and not 3-5, 3-6 or 4-6, as previously reported by various writers. Over half of the embryos observed (62.8 per cent.) showed 4 cotyledons. The mean is $3.69 \pm .03$ when counts are treated statistically. By far the majority of the Redwood (*Sequoia*) embryos had but 2 cotyledons (90.4 per cent.) and the mean obtained is $2.09 \pm .02$, as indicated before. The one abnormal embryo with 4 cotyledons is not included in the data nor shown on the graph, since the small fourth cotyledon arose from a higher point. It was a plumular leaf which made its appearance early.

Thus there is afforded by this type of treatment a more exact statement of measurable differences in terms of constants; it places these differences on a comparable basis; it discloses significant differences when present and is particularly valuable when extremes overlap, such as they do in these two variables of cotyledon number and pollen grain size.

Comparison of dry weights of embryo and endosperm in *Sequoia* in a dozen cases show the embryo to be 36.3 per cent. of the total dry weight; in *Sequoiadendron* the embryo constitutes 40.7 per cent. of the total dry weight. The difference here is small, is based on a very small sample, and is probably not significant. It may be of interest in connection with the work of Clare and Johnstone (1931) on certain pines.

One cone of *Sequoia sempervirens* obtained from cultivation in the Santa Clara Valley yielded a total of 16 embryos, all with 2 cotyledons. This particular yield is much above that obtained from any other locality.

Certain commercial seeds of *Sequoia sempervirens* (collected by Eustice Rush) consisted of only 3 per cent. good seeds. At the rate of 60-80 ovules per cone these would represent a yield of only 1.8-2.5 good seeds per cone. Whether we consider the cone yield in seeds as 16 good seeds per cone (20-26 per cent.) or only 2-3 seeds per cone estimated from the commercial seeds, this rate of seed abortion is extreme in this species and is probably due to the tetraploid condition found in the Redwood.

J. T. BUCHHOLZ
MARGARET KAEISER

UNIVERSITY OF ILLINOIS

LITERATURE CITED

- Blakeslee, A. F., John Belling and M. E. Farnham
1923. *Bot. Gaz.*, 76: 329-373.
- Buchholz, J. T.
1939. *Am. Jour. Bot.*, 26: 535-538.
- Clare, Tema S., and G. R. Johnstone
1931. *Am. Jour. Bot.*, 18: 674-683.
- Davenport, C. B., and M. P. Ekas
1936. "Statistical Methods in Biology, Medicine and Psychology."
New York.
- Gordon, G.
1880. "The Pinetum." New ed. London.
- Hickel, R.
1911. *Bull. de la Soc. Dendrol. de France*, No. 20, pp. 134-204.
- Pilger, R.
1926. "Die Natürlichen Pflanzenfamilien." Engler-Prantl, Leipzig.
- Wodehouse, R. P.
1933. *Bull. Torr. Bot. Club*, 60: 417-421.
1935. "Pollen Grains." New York.

INDUCTION BY FAST NEUTRONS OF MUTATIONS IN
ANTIRRHINUM: II. GENETICS¹

PREVIOUS papers² have reported the effects of fast neutrons on the dry seeds of *Antirrhinum*, *Oenothera*, *Myosotis*, *Ripsalis*, *Echinocereus* and *Neomammillaria*.

In the first paper it was shown that perfectly dry seeds of members of the above genera when indirectly bombarded with fast neutrons resulted, in a number of cases, in decreased germination as well as in marked changes in general morphology upon subsequent planting.

The second paper described how plants grown from the *Antirrhinum* seeds gave rise to flowers which in two cultures were markedly unlike the parent plants from which the seeds were originally obtained. A third culture showed no changes whatsoever with respect to color.

It is the purpose of this paper to record the results of genetic work done on plants grown from seed from the above-described cultures.

Representative plants from each color group in the two cultures showing anomalies were selected for the present work.

¹ Research conducted at the University of Michigan in the departments of botany and physics.

² R. M. Chatters, *Science*, 87: 262-263, 1938; *Science*, 88: 241-242, 1938; *Chronica Botanica*, 4: 391, 1938.

These plants were self-pollinated and the flowers covered with glassine bags to prevent contamination by insect- or wind-borne pollen. The majority of these selected plants failed to set seed.

Plants in Culture No. 2, the progeny of which are being discussed in this paper, were grown from seed which came not only from the same plant but from the same seed capsule. This original plant bore cerise (rose pink) blossoms only.

Two plants which did set seed that later proved to be viable were No. 2/45 and No. 2/69. The former bore burnt orange (called orange-bronze by the writer) and the latter cerise (rose pink) colored blossoms.

Upon planting seeds from these two specimens it was found that many of the seedlings showed the tendency to be dwarfed, weak, and to have mottling on the leaves, as was the case in the parent culture.

Samples of leaves from these new plants were sent to Dr. O. L. Inman, of the C. F. Kettering Foundation at Antioch College, to be tested for any chemical change in the chlorophyll which might possibly have resulted from the bombardment. As in the case of leaves from the parent plants, the results were negative.

Of 100 plants grown from seed obtained from No. 2/45, there were 48 plants bearing burnt orange flowers, and 52 were cerise.

In the case of No. 2/69 there were 74 plants which grew to maturity and flowered. Of this number 21 were burnt orange and 53 cerise.

All the data with respect to color changes due to the bombardment by fast neutrons are summarized in Table I. It is evident

TABLE I

Original <i>Antirrhinum</i> plant	Flower color after irradiating seeds	Color of progeny after self pollination
Culture No. 1 Yellow (lemon yellow)	No change	Not continued
Culture No. 2 Cerise (rose pink)	cerise 48.2 per cent.	} burnt orange . 48 per cent. } rose pink 52 " " } no progeny } " " } " " } cerise 72 " " } burnt orange . 28 " "
	pink "ST" 5.5 " "	
	pink "T" 0.8 " "	
	magenta 1.6 " "	
	burnt orange . 34.7 " "	
	bittersweet ... 9.2 " "	
Culture No. 3 Burnt orange	burnt orange . 54.1 " "	} not continued } no progeny } " "
	bittersweet ... 29.1 " "	
	yellow "L1" .. 4.1 " "	
	spinel rose ... 12.7 " "	" "

from these data that (1) it is not only possible to produce (or

hasten, as one will) mutations by means of fast neutrons, but that (2) these changes may result from the irradiation of *perfectly dry seeds*. Also (3) it is further evident that these mutants after self-pollination will, when viable, produce like progeny in a sufficiently large number of cases as to appear to be significant.

ROY MILTON CHATTERS

WASHINGTON COLLEGE,
CHESTERTOWN, MARYLAND

THE ORIGIN OF AMERICAN TETRAPLOID GOSSYPIMUM SPECIES¹

DENHAM (1924) found the species of *Gossypium* to have either 13 or 26 pairs of chromosomes. The 26-chromosome group is composed of American cultivated cottons and several closely related wild species, which are indigenous to Mexico, South America, Galápagos Islands, and Hawaiian Islands. The 13-chromosome species, which includes cultivated Asiatic cottons, and wild species from Asia, Africa, Australia, Central America, and the Galápagos Islands (Harland, 1939) can be separated into five distantly related types.

Skovsted (1934, 1937) advanced a hypothesis, on evidence derived from chromosome pairing in hybrids and chromosome size, that 26-chromosome *Gossypium* species were allotetraploids with one of the original species similar to Asiatic and the other similar to American 13-chromosome species. Gates (1938) and Webber (1939) were unwilling to accept fully Skovsted's hypothesis, and they considered other possible origins of the tetraploid type.

Obviously, more conclusive evidence of Skovsted's hypothesis could be secured by producing tetraploids that combine American 13-chromosome with Asiatic 13-chromosome species. In the present work tetraploids of this type were produced by doubling the chromosome number in hybrids of *G. therberi* Tod. \times *G. arboreum* var. *neglectum* Hutchinson and Ghose.

The synthesized tetraploid is highly female fertile, but usually the pollen is non-viable. One flower had an abundance of functional pollen which caused seed to develop on the tetraploid and also in crosses with the natural tetraploid form. Hybrids are easy to produce between the synthesized tetraploid and natural tetraploids by using the latter as the male parent.

¹ This work was done while the author was agent, Bureau of Plant Industry, United States Department of Agriculture, Raleigh, N. C.

During meiosis in hybrids between the original species less than half of the chromosomes pair. The bivalents usually gave bridges at anaphase, which is evidence that structural differences existed between all the chromosomes of the two species. After the chromosome number is doubled in the hybrid most of the chromosomes pair, but sometimes multivalents and one or more univalents are present.

The meiotic chromosome behavior in hybrids between the synthesized tetraploid and natural tetraploids is what would be expected according to Skovsted's hypothesis. In meiosis of the hybrid there are usually 24-25 pairs of chromosomes, which leaves 2-4 univalents. In some cells all the chromosomes are paired; there are, however, usually one to three or more multivalent associations. The hybrids will set seeds when self-pollinated, and seeds are produced in reciprocal crosses with the natural tetraploid type. These facts leave no doubt that the American 26-chromosome cottons are allotetraploids, with one parent species similar to existing American 13-chromosome species and the other similar to Asiatic 13-chromosome species. The synthesized tetraploid can be classified as a separate 26-chromosome species, but it is similar in origin and closely related to the natural 26-chromosome species.

An unusual fact about the American tetraploid *Gossypium* species is that one of the parent types is indigenous to the New World, while the other is indigenous to the Old. There can be no doubt that the tetraploid type is pre-Columbian, and Harland (1939) states that the type probably arose in late Cretaceous or early Tertiary.

J. O. BEASLEY

TEXAS AGRICULTURAL EXPERIMENT STATION

LITERATURE CITED

- Denham, H. J.
1924. *Ann. Bot.*, 38: 433-438.
Gates, R. R.
1938. *Empire Cotton Growing Review*, 15: 195-200.
Harland, S. C.
1939. London: Jonathan Cape. 193 pp.
Skovsted, A.
1934. *Jour. Genet.*, 28: 407-424.
Skovsted, A.
1937. *Jour. Genet.*, 34: 97-134.
Webber, J. M.
1939. *Jour. Agric. Res.*, 58: 237-261.

THE SYMBOLIZING OF GENES AND OF CHROMOSOME ABERRATIONS

At the International Congress of Genetics held at Ithaca (N. Y.) in 1932 it was resolved that the genetical societies of all countries should cooperate to prepare recommendations regarding the problem of standardizing genetical symbolism in order to discuss them at the next International Genetical Congress. The International Committee of Genetical Congresses appointed Professor Dr. Tine Tammes (Groningen University) to take charge of the work to be done on behalf of this resolution; in cooperation with Dr. H. de Haan, Miss Tammes prepared a preliminary report on symbolism. Afterwards Miss Tammes delegated the International Union of Biological Sciences to continue her task; in cooperation with the International Institute of Intellectual Cooperation at Paris, the Union convoked a meeting of delegates from various countries, which meeting was held in London in the hospitable home of the Linnean Society on August 14 and 15, 1939. This meeting, under the presidency of Professor Dr. M. J. Sirks (Groningen) was attended by the following delegates: Dr. A. Establier and Miss N. Nicolsky (from the I. I. I. C. at Paris), Professor Dr. Ö. Winge (Denmark), Dr. B. Ephrussi (France), Professor Dr. H. Nachtsheim (Germany), Professor Dr. R. R. Gates, Professor Dr. J. B. S. Haldane and Dr. A. E. Watkins (Great Britain), Professor Dr. K. v. Körösy (Hungary), Dr. K. Ramiah and Dr. S. N. Venkatraman (India), Professor Dr. M. J. Sirks and Dr. S. J. Wellensiek (Netherlands), Professor Dr. O. L. Mohr (Norway), Professor Dr. M. Skalinska (Miss Skalinska, Poland), Dr. O. Tedin (Sweden), Professor Dr. F. Baltzer, Professor Dr. E. Hadorn and Professor Dr. A. Ernst (Switzerland) and Professor Dr. E. W. Lindstrom (U. S. A.); the delegates from Belgium, Italy, Finland and Japan being prevented from attending.

The following rules for symbolizing genes and chromosome aberrations have been drawn up:

Choice of a Standard Type. If it is desired to establish a standard type, this should be the most common form as a wild type or, if such can not be determined, the first studied most dominant form, wild or cultivated.

Symbols for Genes of Standard Type. Generally +; for definite genes preferably the gene symbol with + as a superscript.

Symbols for Other Genes. The smallest possible number of

the initial letters of the name for the character for which Latin is recommended when possible.

Indicating Dominant and Recessive. Dominant, capital initial letter; recessive, small letter.

Multiple Alleles. The symbol of the first discovered allele, in small letters if recessive to standard type, with a capital initial letter if dominant to it. The standard type is designated by the same symbol with + as a superscript; the others by the same symbol with a special superscript in capitals for dominant, in small letters if recessive as compared to the first allele.

Polymeric (Multiple) Genes. Genes which can not be distinguished by the effects and for which the loci are not known are symbolized by the same symbol with different Arabic figures as subscript A_1 , A_2 , A_3 or by the same symbol with the Roman figure of the chromosome as subscript A_I , A_{II} , A_{III} .

Lethal Genes are indicated by the Greek letter lambda (λ) which should be reserved for them, eventually as a subscript to another symbol or separate combined with an Arabian figure with a Roman figure for the number of the chromosome, both as a subscript (λ_1 , λ_2 , λ_3 IV, and so on).

Genes in Polyploids. When the chromosomes form polyvalents or if they pair at random, or if the segregation follows autopolyploid ratios, then the genes are written as many times as they are present, AAA_a , AA_{aa} , A_{aaa} , and so on.

Groups of Linked Genes. The genes written in order from left to right in the chromosome and the symbols spaced II A b c D; between those of different chromosomes a semicolon.

Genes in Related Species. The same symbol but with a subscript of the abbreviation of the specific name.

Formulae. Generally AABbCc, but if parental gametic genotypes are known ABc/AbC and if a linkage group is concerned and the loci of the different genes are known $\frac{a \ b \ c}{d \ e}$, the female gametic genotypes being mentioned first.

Reciprocal Crosses. In case plasmatic inheritance is involved an abbreviation of the name of the mother in parenthesis before the genotypic formula.

Priority shall be valid if no essential objection to the symbol can be made.

Letterttype. Italic for symbols of genes; Roman letters for chromosome aberrations and rearrangements.

CORRESPONDENT

